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PHYLOGENETIC CLASSIFICATION
OF
ANIMALS

HERDMAN



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A
PHYLOGENETIC CLASSIFICATION
OF
ANIMALS

(FOR THE USE OF STUDENTS).

BY
W. A. HERDMAN, D.Sc.,
F.L.S., F.R.S.E.,

PROFESSOR OF NATURAL HISTORY IN UNIVERSITY COLLEGE, LIVERPOOL.

WITH ILLUSTRATIONS.



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PREFACE.

THE accompanying Genealogical Table was drawn up in May, 1884, mainly from various partial schemes of classification which I have been in the habit of using in my lectures for several years; and a brief description was read in the following December before the Literary and Philosophical Society of Liverpool. While preparing this paper for publication* it occurred to me that in an extended form it might prove serviceable to students of Biology: hence its issue in the present condition.

As it is intended to be used along with a good text-book, or as a supplement to a course of lectures on Zoology, no attempt has been made to give the characters of the various groups, and the facts of Anatomy and Embryology are only referred to when they indicate the probable course of Phylogeny. Most attention has been devoted to hypothetical ancestral forms which are rarely, if ever, mentioned in the text-books.

An explanation of the meaning to be attached to the various lines in the table will be found on page 76. The tree-like arrangement is admittedly the best way of representing on a flat surface the affinities of organisms, but it should be remembered that it is after all only a substitute for the model or actual tree, which would much more correctly represent the lines of evolution branching through all the three dimensions of space.

* *Proceedings of the Literary and Philosophical Society of Liverpool* for 1884-85.

Some of my statements in regard to the ancestry or relations of the various groups may doubtless appear very dogmatic. They are not intentionally so, and have been put in a positive form simply to avoid circumlocution and the constant use of "probably," "possibly," and similar expressions.

It is obvious that a classification such as this can only be in a limited sense original. It must of necessity agree in many respects with older schemes, amongst which the well-known diagrams of Professor Haeckel, published first in 1866,* are the most notable of those in a tree-like form.

In working out the details of the table many books have been consulted, and I have tried to incorporate the views of the latest authorities so far as they commended themselves to my judgment. I may expressly mention the extensive use that has been made of various books and papers by Huxley, Ray Lankester, Moseley, Haeckel, Claus, and others; and particularly of that invaluable work, Balfour's *Treatise on Comparative Embryology*.

No one can be more profoundly impressed than I am with the temporary nature of such a table as this. The rapid advances of biological investigation will probably very soon necessitate additions and corrections to any such phylogenetic scheme. The utmost that can be desired is that it should express diagrammatically the present state of knowledge as to the natural classification of animals.

W. A. HERDMAN.

UNIVERSITY COLLEGE,
LIVERPOOL, January, 1885.

* *Generelle Morphologie*. See also *Anthropogenie*, etc., Leipzig, 1877, and *Natürliche Schöpfungsgeschichte*, Berlin, 1879.

A PHYLOGENETIC CLASSIFICATION OF ANIMALS.

IN the following account of the probable Phylogeny of Animals—exhibited diagrammatically in the Table opposite page 76—I have begun with the lowest Protozoa and worked upwards. The Metazoa have been discussed in the following order (the number refers to the page on which the group is commenced):—Porifera (15), Cœlenterata (16), Platyelmia (25), Mollusca (29), Enteropneusta (40), Echinodermata (40), Nematelmia (44), Gephyrea (44), Brachiopoda (44), Polyzoa (45), Chætognatha (45), Rotifera (45), Crustacea (46), Tracheata (51), Discophora (54), Chætopoda (55), Tunicata (58), Cephalochorda (61), Cyclostomata (62), Pisces (62), Amphibia (64), Reptilia (65), Aves (66), Mammalia (66).

At the base of the Table all Animals and Plants are represented as having arisen from a single organism of extreme simplicity, to which the name *Protamœba* is attached. The simplest form of life known to science is Haeckel's *Protamœba primitiva*,* (fig. 1) and it is probable that the first



Fig. 1. *Protamœba primitiva*, Haeckel. Three stages in the life-history, showing reproduction by fission.

formed organism was a particle of unmodified protoplasm,

* Haeckel, *Studien über Moneren*, Leipzig, 1870, p. 43.

which agreed closely with that form in the absence of all visible structure and differentiation. From such an ancestor the derivation of the various Monera now living, and of other allied organisms which have probably existed at different periods, can be readily imagined to have taken place by slight changes of form, habit, and life-history, effected by means of natural selection. It is quite possible that some existing or extinct groups of lowest organisms may have arisen independently of others, but there is no evidence in favour of this "polyphyletic" arrangement, and therefore it is simpler to understand, and on the whole more probable, that all forms of life have been derived from a single common ancestor. When once a particle of living protoplasm had, under certain conditions of which we are absolutely ignorant, become evolved from inorganic materials, there would be no need of any further points of origin. The various Protista (the lowest animals and plants) can all be satisfactorily regarded as being derived from one another, or from hypothetical intermediate forms.

The line leading straight* upwards from *Protamœba* to near *Protomyxa* is supposed to run through a series of ancestral Monera which were successively less and less absolutely undifferentiated, and from which many side branches (long or short, according to the amount of variation displayed) have diverged. The few of these which are shown in the table may be taken as representing some of the more important groups of Monera which are known. The intermediate forms have become extinct.† The table would be a more correct representation of nature if every line and branch had been shown bristling with innumerable short twigs, extending in all directions, of different lengths, and many of

* All the straight lines in the table must be regarded as very fine zig-zags, since each ancestral form diverged a little from its predecessor.

† In regard to this, consult *The Origin of Species*, 6th ed., p. 293.

them branched, and giving off twigs in their turn. These would represent different slight modifications or varieties, most of which have died out. They would have added greatly to the complication of the table, and can readily be imagined, therefore they have been omitted.

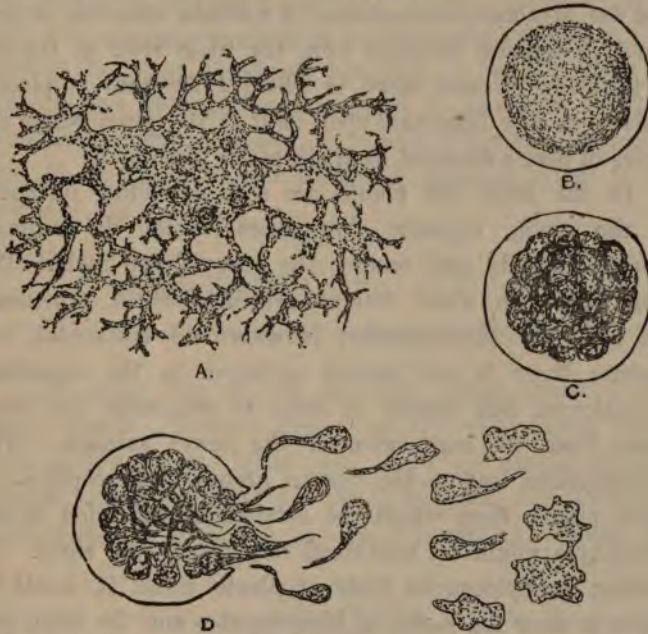


Fig. 2. *Protomyxa aurantiaca*, Haeckel. A. The plasmodium stage. B. The encysted condition. C. The protoplasm inside the cyst breaking up into mastigopods. D. The mastigopods, set free by the rupture of the cyst, becoming myxopods, and then uniting to form small plasmodia.

Protomyxa (fig. 2) is decidedly above *Protamœba* and others of the Monera, and has a complicated and very instructive life-history,* the main points of which are that a myxopod stage (the plasmodium, fig. 2, A) passes into an encysted condition (fig. 2, B), and then breaks up into a number of mastigopods (fig. 2, C), each of which after escaping from the cyst becomes a myxopod (fig. 2, D).

* See Haeckel, *Studien über Moneren*; or, Huxley's *Invertebrata*, p. 81.

These then fuse together, in small numbers, to form plasmodia, such as the first stage, and thus complete the cycle. The life-histories of many of the Myxomycetes exhibit series of stages very closely resembling those just enumerated, and therefore it is probable that *Protomyxa* and the Myxomycetes possessed a common ancestor, or that the Myxomycetes diverged from the main stem at the top of the Monera, and close to where *Protomyxa* is placed. This is a very important spot, as it is the place where the series of plants diverged from the series of animals.

In the table, the plants are seen extending outwards to the right, opposite *Protomyxa*, while the animals extend upwards and occupy the rest of the table. The long line with short lateral branches which represents the series of Myxomycetes, is shewn as horizontal, not because there is no upward evolution in the organisms it indicates, but simply in order to emphasise its divergence from the main stem of the lower animals. The Myxomycetes lead to the various groups of Protophyta, or lower plants, from which the detailed classification of the Metaphyta might be continued onwards to the right. In making a phylogenetic table of plants alone, it would be better to show the series of Myxomycetes and the main axis of the Protophyta more in a straight line with the Monera; and in a scheme embracing all organisms the main stems of the plants and the animals should be made to diverge at nearly equal angles from the common ancestor, close to *Protomyxa*.

The rest of the lower animals, from *Protomyxa* up to the first dotted line running across the table, are the Protozoa, and may be considered as comprising four great groups, which diverge from the main stem, two of them, the Infusoria and the Gregarinida, near to *Protomyxa*, and the other two, the Foraminifera and the Radiolaria, near to *Amœba*, further up.

The large and rather heterogeneous group of organisms, known as Infusoria,* may be traced back to a point of origin at the top of the Monera, and the ancestral forms were probably simple Monads, resembling closely the mastigopod stage in the life-history of *Protomyxa*. If one of the doubtless numerous varieties of *Protomyxa*-like organisms, which have existed, had its mastigopod stage emphasised, so as to become the most important condition in its life, while the other stages were partly suppressed or modified, it would gradually become a Monad, or simple Flagellate Infusorian (fig. 3), and such was probably the mode of origin of this group of the Protozoa.



Fig. 3. A Monad, one of the Flagellate Infusorians.

The main line of the Infusoria leads upwards from these simple ancestral forms to the very much higher and more complex Ciliata; but there are several aberrant groups, such as some of the Flagellata, the Catallacta (*Magosphæra*), *Noctiluca*, and allied forms, which must have



Fig. 4. *Magosphæra planula*, Haeckel. Optical section of the colonial stage in the life-history.

diverged from the axis far back, and have become evolved in different directions. *Magosphæra* (fig. 4) exhibits affini-

* For figures of this group, the student should consult Saville Kent's *Manual of the Infusoria*.

ties with *Protomyxa*, and with the Flagellata, but is more highly differentiated; while some of the Cilioflagellata (*e.g.*, *Peridinium*) shew such striking resemblances to some of the lower plants that it is a question with some biologists whether or not they belong to the animal series. But the resemblances are really not surprising when we consider the close relationship between the lower Infusoria and the Proto-phyta. The common *Protomyxa*-like ancestor is not far removed from either of them.

In passing up to the higher Infusoria, we find that the Holotricha (*e.g.*, *Paramœcium*)—where besides internal differentiation, the body has acquired a uniform covering of cilia—are most nearly in the direct line of development (*i.e.*, are most nearly allied to the probable ancestral forms), and may be regarded as the central group of the Ciliata. The Hypotricha, the Heterotricha, and the Peritricha, are more or less divergent groups, in which the cilia do not form a uniform coating, and they may be conveniently represented as being at the ends of side branches from ancestors of the Holotricha. The Peritricha (*e.g.*, *Vorticella*) are probably further removed from the main line than any of the others. The Opalinida, a small group of parasitic Infusoria, found in the intestine of some Amphibia, may be regarded as having degenerated from the Holotricha, which they resemble in the arrangement of their cilia.

The Tentaculifera (or Suctoria, *e.g.*, *Acineta*) are a rather isolated group, the exact relations of which are difficult to determine. Saville Kent traces them back to a point on the main axis of the Protozoa, near to *Amœba*, but it is more probable that they have diverged from the stem of the Infusoria, distinctly below the Ciliata, as shown in the table. They are placed on a long side branch, which does not rise much in its course. This indicates that they are

considerably divergent, but have not attained such a high grade of organisation as is found in the Ciliata.

So many modifications of form and structure occur in the higher Infusoria, and so many of these are intermediate or transition forms between the different groups, that it is comparatively easy to imagine the process of evolution, and to trace the course by which common ancestral forms became gradually modified through successive generations into Heterotricha on the one hand, or Peritricha on the other, or were slowly degraded into the Opalinida. Before leaving the Infusoria, it is well to notice the great range of organisation in the group. The difference between such a simple form as one of the Monads, and such a highly differentiated Protozoon as *Paramœcium*, or *Euplotes*, or *Stentor*, or *Vorticella* is very great. This is indicated in the table by the length of the line from the point of origin to the top of the Peritricha. It is greater than that of any other group of the Protozoa.

The Gregarinida,* like all parasitic organisms, are difficult to place, as there is always a probability that they have been considerably modified, or even degraded from the ancestral type, in consequence of their habits. They are placed in the table at the end of a long branch springing from the main stem of the Protozoa, close to the highest Monera, and extending outward and upward so as to reach a point a little above the level of *Amœba*, but far from the axis. The length of the line shows the considerable amount of differentiation attained by the group† and its somewhat isolated position, while its point of origin indicates the relationship which probably exists with the Monera. There is a similarity with the life-history of *Myxastrum*,‡ and the ancestors of the

* E. van Beneden, *Bull. de l'Acad. Roy. de Belgique*, 2nd ser., T. xxxi.

† E. van Beneden, *Bull. de l'Acad. Roy. de Belgique*, 2nd ser., T. xxxiii; and *Quart. Journ. Mic. Sc.*, new ser., vol. xii, p. 211.

‡ Haeckel, *Studien über Moneren*, or Huxley's *Invertebrata*, p. 79.

Gregarinida may have diverged from the other Protozoa at a point close to this form, or one of the other allied Monera. On the other hand, it is possible that the Gregarinida may have degenerated from one of the higher Protozoa—from some form above *Amœba*—or even from still higher animals. The dotted line in the table, stretching downwards from the base of the Metazoa, may serve to recall the possibility that the Gregarinida are a much degraded offshoot from some group of Gastrea-like organisms.

The two remaining large groups of the Protozoa—the Foraminifera and the Radiolaria—may be satisfactorily traced back to ancestors which must have been closely allied to *Amœba*. As it is improbable that *Amœba* has remained absolutely unchanged since the time when the Foraminifera and Radiolaria diverged, it has been placed in the table not on the main line but upon a short side branch considerably above the Monera. The ancestral forms which occupy the axis between *Protomyxa* and the point nearest to *Amœba* must have gradually acquired a well-marked endoplast, while at the same time, the protoplasm became more and more differentiated into two layers, the ectosarc and endosarc, in the former of which a contractile vacuole* was developed. It is possible that the Amœbidæ, the Foraminifera, and the Radiolaria may all have had a common ancestor from which the three lines started.

Taking the Foraminifera first, we can trace their origin from the Amœba-like form on the main stem through the ancestral Lobosa. The stages by which a shell of some kind

* Possibly this structure was not present in the ancestral forms, and has been acquired since by *Amœba*, *Actinosphaerium*, &c. I think that the contractile vacuole in the higher Infusoria must be regarded as having been evolved independently in that group. The only alternative is to place the point of origin of the Infusoria much higher up on the main axis, above an ancestral form possessing a contractile vacuole, and to consider the lower Infusoria as degraded forms.

was first acquired may readily be understood by passing from the common *Amœba* to forms where the pseudopodia are restricted to one part of the surface; and then to *Diffugia*, where the rest of the body is enclosed by a case formed of small sand grains, picked up and attached by the protoplasm; and *Arcella*, where a delicate shell of a chitinous nature is secreted by the surface layer of protoplasm. In such forms the pseudopodia are still short and thick, as in *Amœba*, but

change from these to the higher Foraminifera, where pseudopodia are long and delicate, is a slight one, which may be readily understood. Finally, the Foraminifera have branched out into a large number of modifications which differ comparatively little from one another.

In tracing the history of the Radiolaria, we start from the same point as that occupied by the ancestral Foraminifera, but diverge in a different direction. If we imagine an *Amœba*-like form becoming more and more regularly spherical in shape, while the pseudopodia get longer and thinner and more regularly arranged, and the ectosarc becomes more clearly distinguishable from the endosarc, we shall have it gradually passing into an ancestral Radiolarian or Heliozoon (such as *Actinosphærium*), for Haeckel has shown* that the four existing groups of Radiolaria, the Sphaerulophoria, the Spumellaria, the Nassellaria, and the Phaeodaria, may be traced back to a common ancestor, which agrees in all particulars with an ancestral Heliozoon in which the endosarc has become separated from the ectosarc by a membrane, thus forming a central capsule. This form, to which Haeckel has given the name *Actissa* (fig. 5), is so closely allied to *Actinosphærium* that it is certain the two forms must have had a common ancestor not far back, and only differing from *Actissa* in having no capsule membrane. The Heliozoa of the present day split off at this point, and

* See *Nature*, vol. xxix, pp. 274 and 296. 1884.

have remained at much the same level of organisation, while the main line continued upwards to *Actissa*. A side branch from this point leads to *Actinelius*, the ancestral form of the Acantharia. This was derived from *Actissa*, according to

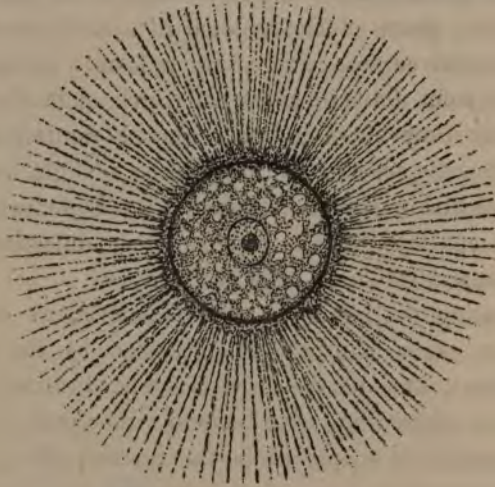


Fig. 5. *Actissa* (after Haeckel).

Haeckel, by the hardening of the firmer axial part of the radiating pseudopodia into spicules of acanthin, the only form of skeleton found in the Acantharia. The central capsule in this group remains simple and spherical, and is pierced on all sides by fine pores.

The Spumellaria are more nearly in the direct line of development than the other three groups, and may be traced back to *Actissa* as an ancestral form. The central capsule remains in its simple form, but most of the Spumellaria have acquired a siliceous skeleton, or shell, which serves to distinguish them from the Acantharia. The Nassellaria have diverged from the primitive Spumellaria, their probable ancestor *Cystidium* being derived from *Actissa* by the pores of the capsule membrane becoming

restricted to an area situated at one of the poles in place of being scattered equally all over. The Nassellaria agree with the Spumellaria, and differ from the Acantharia in possessing a siliceous skeleton.

The Phæodaria are the most divergent and most highly differentiated group of the Radiolaria. They may be considered as derived from *Phæodina*, an ancestral form which has arisen from *Actissa* by a considerable amount of modification. The capsule membrane became double, and the pores probably first became restricted to one pole, and then this porous area was modified into a single opening provided with a radiated operculum. Two small accessory openings at the opposite pole of the capsule may also be present. A peculiar pigment body (the phæodium) became developed outside the capsule membrane, close to the principal opening. These characters are found throughout the Phæodaria, and the majority of the group possess in addition a skeleton formed of hollow siliceous bars, a feature distinguishing them from all other Radiolaria.

The Metazoa, to which we must now pass on, includes the animals above the Protozoa, and may be distinguished by two important characteristics:—1. The body is always multicellular, being formed of more than one cell, usually of a very large number. The few Protozoa which are composed of more than a single cell (such as some of the Infusoria—see fig. 6), are clearly colonies formed of a number of independent members, each of which is unicellular. 2. Reproduction, though it may also be effected by budding, or some other asexual method, is always performed sexually by ova and spermatozoa; while in the Protozoa, these reproductive elements are not found, and consequently true sexual reproduction cannot take place. These two characters might be considered as one, since the second really depends upon the

first. As the sexual elements are equivalent to cells, they can obviously only be produced in a multicellular body.

As to the method by which the unicellular Protozoa became multicellular Metazoa, it is probable that the passage



Fig. 6. *Magosphera planula*, Haeckel. Optical section of the colonial stage in the life-history.

was effected by some unknown colonial forms which may be placed above *Amœba*. This is a more probable position for the transition forms to occupy than the tops of any of the Protozoa groups, such as Infusoria, or Foraminifera, or Radiolaria would be, and the line stretching straight upwards from near *Amœba* may be supposed to pass through the hypothetical compound Protozoa. In the development of any one of the Metazoa, we see a unicellular organism



Fig. 7. Blastula stage in the development of a Metazoon.

becoming multicellular (*e.g.*, the blastula stage seen in fig. 7), but the exact process differs considerably in different groups, and there is great difficulty in determining in which

case the ancestral evolution is most closely followed. Consequently, although it is generally admitted that some embryonic stages in the development of Metazoa probably repeat the unknown transition forms, still there is great difference of opinion amongst zoologists as to which embryonic forms actually represent the ancestral Metazoa. Haeckel* has founded upon the prevalence of the embryonic stage known as the Gastrula (fig. 8) throughout many

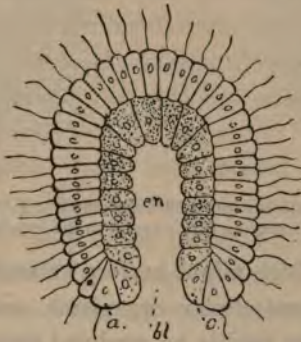


Fig. 8. Gastrula stage in the development of a Metazoon; a, epiblast; c, hypoblast; bl, blastopore; en, archenteron.

groups of the Metazoa, his "Gastrea" theory, which is, that the Gastrula stage in embryology represents the Gastrea, an ancestral organism formed of two layers of cells, the outer epiblast and the inner hypoblast, enclosing a central cavity which communicates with the exterior at one end (see fig. 8). Lankester,† on the other hand, considers that the Planula (fig. 9), an embryo formed like the Gastrula of two layers of cells, but differing from it in having no opening, is more probably the far back common ancestor of the Metazoa. Recently Butschli‡ has brought forward arguments in favour of the "Placula" (fig. 10)—a simple

* *Studien zur Gastræa-theorie*, Jena, 1877.

† *Notes on Embryology and Classification*. London, 1877.

‡ *Annals and Magazine of Natural History*, for May, 1884.

flat plate or disc formed of two layers of cells, the upper epiblastic and the lower hypoblastic—being regarded as the earliest common ancestor of the Metazoa. The Placula is

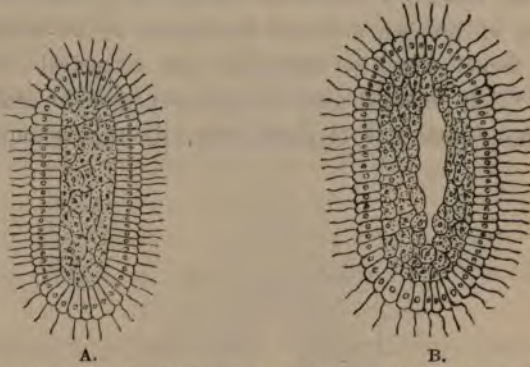


Fig. 9. Planula stage in the development of a Metazoon; A, planula with solid hypoblast; B, planula with a cavity in the hypoblast.

certainly a form which might be very naturally assumed by a small colony of unicellular organisms, and Butschli has shown how it might readily be modified during its formation so as to assume either a Planula or a Gastrula structure.

From the early Metazoon represented by one of these, or some closely related embryonic form (the point marked *Gastrea* in the table), several lines must have diverged.



Fig. 10. Placula—a hypothetical ancestral form (after Butschli). Two stages in its development are shewn.

One of these, on the right, slopes considerably downwards to end in the Dicyemida and the Orthonectida. These two lowly organised groups are parasitic, and probably degenerate. They agree with the Metazoa in being multicellular, but differ from them in having the endoderm represented by a single cell only, and they have some peculiarities in regard

to their reproduction. On these grounds they have been distinguished by E. van Beneden,* and others, as Mesozoa. Probably they are merely degraded and modified offshoots from an early group of the Metazoa.

The two great series of the Sponges, or Porifera, and the Cœlenterata, probably diverged from the main stem, close to Gastrea, at or near the same point, or possibly they may have arisen together by a short side branch representing a few common ancestors after they had left the main stem. It is possible, on the other hand, that the Porifera may have arisen from a group of the higher Protozoa, independently of the other Metazoa.† In this case, they would have no close relationship with the Cœlenterata.

The Physemaria‡ have been placed upon a separate branch, close to the base of the Porifera, and arising from Gastrea. This is the position assigned to them by Haeckel, who described them§ as simple Gastrea-like organisms, related to the lowest Sponges; but more recent investigations by Ray Lankester,|| and others, have thrown very grave doubts upon this interpretation of their structure, and it is not improbable that they may all turn out to be merely large and somewhat abnormal Foraminifera.

The ancestral Sponges probably divided at an early period in the history of the group, into two series, now represented by the forms with calcareous spicules and the rest. The simplest calcareous Sponges (Haeckel's Ascones) may be distinguished as Homocœla,¶ from the more complex forms (the Sycones, the Leucones, and the Teichones) or Heterocœla.

* "Recherches sur les Dicyemides," *Bulletin Acad. Roy. de Belgique*, 1876.

† See Balfour, *Comp. Embryol.*, v. ii, p. 285.

‡ Haeckel, *Jen. Zeitsch.*, Bd. x, and Huxley's *Invertebrata*, p. 645.

§ *Studien zur Gastrœa-theorie*, iii, *Die Physemarien*.

|| *Quart. Journ. Micros. Sc.* vol. xix, p. 476, 1879.

¶ Poléjaeff, "*Challenger*" *Zoological Reports*, vol. viii, Part xxiv (1888).

The remaining groups of the Porifera have become considerably modified from the primitive ancestor, and their phylogeny is not very clear. The Myxospongiæ, in which no spicules are present, are probably the least differentiated, but may have degenerated somewhat, as is shewn by the line in the table sloping slightly downwards. The great group of the Fibrospongiæ, in which an extensive skeletal apparatus, formed of kerotose fibres, and generally of siliceous spicules also, is developed, have diverged with a considerable amount of differentiation from a still more advanced point, leaving the Hexactinellidæ (the vitreous sponges) as the termination of the Porifera branch, and farthest from the main stem of the table. The Fibrospongiæ have split up into a large number of smaller groups.

The great series of the Cœlenterata arose from *Gastrea*, the sac-like ancestor, with its wall formed of two layers of cells, and having a central cavity and a mouth opening (see fig. 11). Some of the descendants of this form diverged

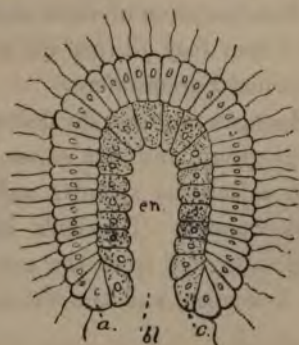


Fig. 11. Gastrula stage in the development of a Metazoon; *a*, epiblast; *c*, hypoblast; *bl*, blastopore; *en*, archenteron.

from the primitive Sponges on the one hand, and from the ancestors of the higher Metazoa on the other, and by the development of tentacles or outgrowths from the body,

formed by both cell layers, became the more immediate progenitors of the Cœlenterata. The organism* which occupied the point where the Cœlenterate branch first divided was probably a short, wide, sac-like form, fixed by its aboral end, and having large tentacles in multiples of four placed equatorially, and possibly also smaller tentacles around the mouth opening (fig. 12, A). This form, probably, on becoming

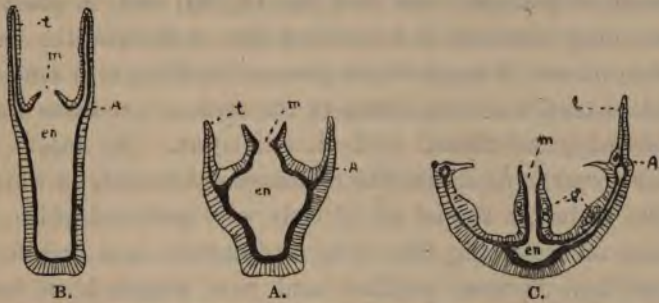


Fig. 12. Primitive Hydrozoa. Three diagrammatic vertical sections (after Lankester). A, Ancestral Hydrozoan shewing a condition intermediate between the Hydra-form and the Medusa-form. B, Simple Hydra-like ancestor produced by modification of A. C, Simple Medusa-like ancestor produced by modification of A. *m*, mouth; *en*, enteron; *t*, tentacle; *g*, reproductive organs. *A*, Indicates the same point in each form, viz., the base of the tentacle. In A it is at the equator of the globose body, in B at the top of the cylindrical body, and in C at the margin of the bell-shaped body. The dark inner-wall of the enteron is the endoderm, the lighter outer layer of the body is the ectoderm.

sexually mature detached its base, and, by enlarging its equatorial region into a disc, and finally into a bell concave on the oral face and provided with circularly-placed bands of muscle, acquired a swimming organ by the contractions of which it could be propelled through the water (see fig. 12, C). The ova and spermatozoa were then developed upon the inner walls of the enteric cavity of this Medusa-like form.

This common ancestor of all the Cœlenterata (which is most nearly represented at the present day by the Hydra-

* See Ray Lankester's article, "Hydrozoa," in *Ency. Brit.*, 9th edition, p. 552.

tuba stage in the development of the Discomedusæ) must have given rise to two divergent series of forms—the one the ancestors of the Hydromedusæ and the Ctenophora, and the other the ancestors of the Scyphomedusæ and the Actinozoa.

In the first series the hydriform fixed stage became emphasised, the body became longer, and the enteric cavity remained a simple tube (see fig. 12, B); and, in place of becoming detached and modified into a Medusa-like form when mature, it acquired the power of budding to a remarkable extent, the buds being in the form of processes from the body, and formed of both cell layers. By means of this property, fixed tree-like colonies were formed, on which, after a time, a special set of buds were produced which, in place of remaining like their predecessors in a hydriform condition, became modified and were detached as free-swimming medusiform persons in which the reproductive elements were developed. This specialisation of the two sets of buds in the common ancestor of the Hydromedusæ brought about the state of affairs generally known as "alternation of generations." The ovum of the medusiform person develops into a hydriform person which produces by budding a tree-like colony upon which certain buds become medusiform persons, are detached, and produce ova and spermatozoa.

In the ancestors of the Trachylarida the life-history became simplified, probably by the hydriform fixed stage being more rapidly hurried over until it came to be of little importance, and was finally suppressed altogether—the result being that in that group (including the Trachomedusæ and the Narcomedusæ) at the present day we find the ovum developing directly into the Medusa.

On the other hand, in many of the Calyptoblastea and Gymnoblastea, we find that the medusiform persons become

modified by developing their reproductive organs while still attached to the hydriform colony; this results in their ceasing to become detached, and in some forms they become more and more degenerate, until eventually the sporosacs of *Hydractinia*, and the simple reproductive organs of *Hydra*, are reached.

In the Hydrocorallina and some Gymnoblastea, "polymorphism" has added greatly to the complication of the colony. We find various sets of buds developing into differently shaped persons which are specially fitted to perform certain functions in the colony. In *Hydractinia*,* for example, there are nutritive persons, reproductive persons, tentacular persons, and defensive persons in the one colony.

On its outer surface, in the hydriform person in many of the Hydromedusæ, the ectoderm (the outer layer of cells) forms a horny layer, the perisarc. This may be very slightly developed and confined to the aboral end, or it may cover the entire body and project beyond the oral region in the form of a calycle or hydrotheca, and cover groups of medusiform buds as a gonangium (as in the Calyptoblastea). The Hydrocorallina probably diverged from the base of the Gymnoblastea, their ancestors having acquired the property of forming calcareous deposits in the ectoderm, so as to produce a hard, stony corallum. Polymorphism is found here in an advanced condition.

The Siphonophora diverged from the ancestral Hydromedusæ, and acquired the characteristic of never becoming fixed at any period of their life-history. Probably at an early point in their independent history the hydriform person developed from the ovum commenced to bud while very young, and produced medusiform persons before becoming fixed. The result of this would be that the pulsations of

* Allman's *Gymnoblasic Hydroids*, Part ii, p. 220, Ray Soc., 1872.

the Medusæ would propel the entire colony, consisting of both hydriform and medusiform persons, through the water, and locomotion being thus effected, it would be unnecessary for the medusiform persons to become detached. Then polymorphism produced changes in both the hydriform and the medusiform persons, resulting in the very complicated free-swimming colonies of Siphonophora found at the present day.

The Ctenophora were probably derived from an ancestral Hydromedusa near to the common ancestor of the Gymnoblaster and the Siphonophora. The primitive Ctenophora must first have lost their hydriform stage in the same manner as it was lost by the ancestral Trachylarida. This would result in their becoming free-swimming Medusæ, like the medusiform persons of the Gymnoblaster, but differing from them in developing directly from the egg. They must then have undergone a series of changes which may be seen partly effected in the remarkable transition form described by Haeckel as *Ctenaria*, which resulted in the narrowing of the margin of the bell so as to produce a nearly spherical form with a small mouth opening (as in *Pleurobrachia*), and in the formation of eight bands of modified ciliated ectoderm running meridionally down the outside from pole to pole. The enteric cavities also became modified, and the tentacles were reduced to two, and became retractile into laterally placed sacs. The evolution of the various groups of Ctenophora from a *Pleurobrachia*-like common ancestor is easy to trace.

Returning to the common ancestor of all the Cœlenterata, we find that the second series of forms diverging from this point leads to the primitive Scyphomedusæ and Actinozoa, and is characterised by the hydriform stage remaining simple and single in place of producing a colony. It acquired, however, the power of giving off pieces of its body as buds,

each of which developed into a free-swimming Medusa-like form, in which reproductive elements were produced. We see this ancestral process repeated at the present day in the life-history of the Discomedusæ (*e.g.*, *Aurelia*), where the Scyphistoma stage (hydriform person) produces by transverse fission a number of Ephyrae (medusiform persons). In some Scyphomedusæ (*e.g.*, *Pelagia*), the hydriform stage has become suppressed, and the ovum develops into a Medusa directly, just as it does in the case of the Trachylarida.

The ancestral Scyphomedusa must have developed solid tentacle-like filaments projecting from the body wall into the enteric cavity, as we find such gastral filaments* present in all members of the Scyphomedusæ. The Lucernarida are probably more in the direct line of development than any of the other Scyphomedusæ, as they have retained an intermediate condition between a Hydra and a Medusa form. They do not produce Medusæ by transverse fission (strobilation), but develop genital organs from the endoderm.

The Discomedusæ are the typical large Medusæ, with often very complicated sense-organs (modified tentacles) around the margin of the bell. The mouth may remain simple or become greatly complicated (in the Rhizostomæ).

The Cubomedusæ and Peromedusæ are two small groups, which differ from the Discomedusæ and from each other mainly in the arrangement of the sense-organs and the enteric cavities. They probably diverged from the base of the Discomedusæ.

The Actinozoa were in all probability derived from the ancestral Scyphomedusæ, but they have attained a more advanced condition both as regards their internal cavities and also their general histology than is found in any of the Hydrozoa (Hydromedusæ and Scyphomedusæ). Con-

* Haeckel's "Phacellæ," "Challenger Zoological Reports, vol. iv, part xii. The Deep-Sea Medusæ, Introduction, p. lxxiii.

sequently a considerable space must be allowed between their point of origin from the Scyphomedusæ and the immediate common ancestor of the Zoantharia and Alcyonaria. This form, which must have been polype-like in appearance (the medusiform condition having been finally lost some way back), was intermediate in its characters between a Sea-Anemone and a simple Alcyonarian, but less differentiated than either. It must have possessed the typical Actinozoon arrangement of internal cavities—a stomodæum or gastric tube, and an enteron sub-divided by radiating mesenteries—as this structure is found in both the Zoantharia and the Alcyonaria. It probably had the power of budding off polypes like itself, which were not free-swimming, but remained fixed to the parent form. From this “Proto-polype” two ancestral series must have arisen, the one leading onward to the Proto-Alcyonaria, and through them to the various groups of Alcyonarians now known, and the other diverging to become the ancestors of the Antipatharia, the Actiniaria, and the Madreporaria.

The Proto-Alcyonaria must have acquired the character of having only eight tentacles and the same number of mesenteries, while the tentacles became more or less pinnate or fringed. This ancestral stock is most nearly represented at the present day by such simple Alcyonaria as the genera *Monoxenia*, *Haimea*, and *Hartea*; while the remaining Alcyonarians have advanced from this point along two divergent series—the one branch (to the right in the table) leading through such forms as *Sarcodictyon* and *Clavularia* to the Tubiporidæ, and the second forming the common stem from which the ancestral Helioporidæ, Alcyonidæ, Gorgonidæ, and Pennatulidæ, have arisen. In the first of these series the property was acquired of forming calcareous deposits in the mesoderm (or deeper layer of the ectoderm) of the body wall. They are found in the form of detached but

numerous spicules in *Sarcodictyon*,* and united to form a continuous tube in *Tubipora*. †

The four families forming the second series have been differentiated in different directions, and differ from one another mainly in their methods of budding to form colonies, and in the kind of skeleton they produce. The Helioporidæ are remarkable on account of their having twelve tentacles and a peculiar corallum which shows certain resemblances to the skeleton in the true corals or Madreporaria, a group with which the Helioporidæ have no direct relationship. ‡ In the Alecyonidæ the skeleton is in the form of scattered spicules, while in the two remaining families, the Pennatulidæ and the Gorgonidæ, a solid axis is formed which traverses the centre of the colony. In the Pennatulidæ the colony is of elongated form, and the axis is unbranched; while in the Gorgonidæ both are frequently of complicated and tree-like forms.

The second diverging series of forms from the Prototype, must have acquired the characteristic of having the tentacles simple and in multiples of six, since those conditions are found in the Antipatharia, and in nearly all Actiniaria and Madreporaria. The ancestors of the Antipatharia probably were the first offshoots from the primitive Zoantharia, and in their descendants at the present day we find a form of skeleton developed which differs from that of all other Zoantharia, and agrees with that of most Alecyonaria, in being an axial rod. The primitive Zoantharia must then have split up into two series, of which one was the stock of the Actiniaria, and the other of the Madreporaria. The ancestors of the Sea-Anemones lost the habit of reproducing by gemmation, and formed no hard skeleton of any

* Herdman, "On the Structure of *Sarcodictyon*," *Proc. Roy. Phys. Soc., Edin.*, vol. viii, p. 31 (1883).

† Hickson, "On the Structure and Relations of *Tubipora*," *Quart. Journ., Mic. Sc.*, vol. xxiii, No. xcii, p. 556 (1883).

‡ Moseley, "Challenger" *Zoological Reports*, vol. ii, part vii, p. 102.

kind. The tentacles and mesenteries have become very numerous in most of the forms existing at the present day.

The ancestral Madreporaria, on the other hand, must have acquired the property of producing a calcareous skeleton which was not confined to the axis of the colony, as in the Aleyonaria and the Antipatharia, but was developed in the mesoderm, not only of the colony, but of the polypes also, so as to form a skeleton for each member of the colony. In most of the groups of Madreporaria now existing, reproduction by budding takes place to a great extent, large and complicated colonies being the result.

Returning now to the main stem of the tree, we find that above Gastrea it passes up into that intensely interesting region which is the origin of the various groups of lower Vermes. From this it may be traced upwards through the starting points of all the great groups of higher Metazoa, the Mollusca and the Chordata, the Crustacea and the Tracheata, to its termination in the Polychæta—the highest Vermes. From Gastrea to the base of Polychæta then, the main axis of the tree may be considered as consisting of a series of ancestral worm-like forms extending from the most primitive, the first modification of a Gastrula, up to the immediate progenitors of the higher Annelides.

What the changes were by means of which the Gastrea passed into one of the ancestral lower Vermes is difficult to determine. The body probably became elongated, and a mesoderm was developed between the two primary cell layers; but whether the elongation took place along the antero-posterior axis of the Gastrea, so that the aperture remained as a terminal mouth-opening, or at right angles to that axis, so as to convert the aperture into an elongated slit placed upon one surface, is a disputed point. Balfour* and

* *Comp. Embryol.*, vol. ii, p. 308.

Sedgwick* have advocated the derivation of all the higher Metazoa from a form having the aperture pulled out at right angles to the axis, and more or less dilated at its angles, as in many of the Actinozoa, and characterised also by having its enteron prolonged into a series of radially placed diverticula resembling the intermesenteric spaces of the Actinozoa. Such a structure might readily be produced by modifications of *Gastrea* (see fig. 13), and there are strong arguments in

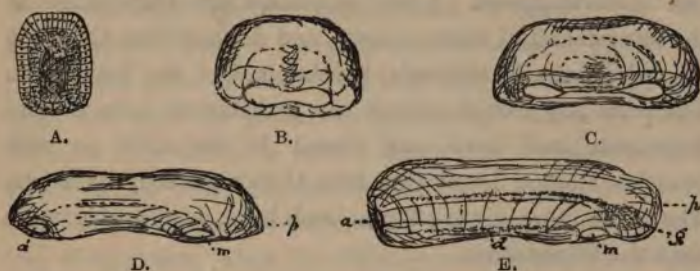


Fig. 13. Hypothetical forms shewing stages in the conversion of the Gastrula into a primitive worm. A, Gastrula. B, Elongation has taken place along a line at right angles to the long axis of the Gastrula, and the opening is becoming reduced to a slit dilated at the ends. C, Further elongation has taken place, and the original Gastrula opening is now converted into two apertures (the mouth and the anus), united by a curved tube, formed by the archenteron of the Gastrula. D, The anus has moved further back, and the alimentary canal has become longer and straighter. E, The diffused nervous system has commenced to be concentrated in the anterior part of the body in front of the mouth, and as two longitudinal bands running along the sides of the body. *a*, anus; *m*, mouth; *p*, præ-oral lobe; *g*, supra-oesophageal ganglion; *d*, lateral nerve cord.

favour of the first ancestral Vermes having had such an arrangement, but it is very improbable that it was related in any way to the similar structures in the Actinozoa, and must have been acquired independently.

The groups of lower Vermes usually united under the term *Platyelmia*,† are represented as springing from the main

* *Quart. Journ. Micros. Sc.*, vol. xxiv, No. xciii., p. 43 (1884).

† Lang (*Mittheil. Zool. Stat. Neapel*, Bd. iii. p. 187, 1882; and *Fauna und Flora des Golfes von Neapel*, XI. Monographie: Die Polycladen, p. 645, 1884) tries to show that the lower Vermes have been evolved from the Ctenophora, a course which seems very improbable and will require a great deal of evidence in its favour before it can be accepted.

stem by a common root, from which the group Cestoda is given off. The existing forms are placed at the end of a line which is long, to indicate considerable divergence from the ancestral form, and slopes downwards to show that the group is a degenerate one.

The Dendrocœlous and Rhabdocœlous Turbellaria are probably the least modified members of the Platyelmin branch, and are therefore placed most nearly in the direct line of development. Lang* considers the Polycladidæ as the most ancestral forms known, and derives from them the Tricladidæ, the Rhabdocœla, the Accœla, and the Trematoda. The three last named groups are probably all more or less degenerate and have been placed in the table on side branches sloping downwards from the ancestral Dendrocœla. The Accœla were given off first and have degenerated more than the Rhabdocœla.

The Trematoda are more divergent than any of the Turbellarian groups. They show affinities in structure both with the Dendrocœla and with the probable ancestral form of the Cestoda. Probably they diverged from the Dendrocœlous Turbellarians, and have been considerably specialised and somewhat degraded. As a result of their generally parasitic habits they have lost their original coating of cilia and have acquired various organs of attachment.

The Nemertida are the highest group of the Platyelmia. They probably arose from the ancestral Turbellarians very far back and seem to have undergone a considerable amount of evolution. The body is elongated and more worm-like than in the other Platyelmia, and the alimentary canal is more highly differentiated. An anal opening is present, and a protractile frontal proboscis, often of very large size and armed with chitinous styles, is a characteristic feature.

* *Fauna und Flora des Golfes von Neapel*, XI Monographie: Die Polycladen.

The nervous system, which in the ancestral *Platyelminth* was probably diffused over the general surface, with perhaps a tendency towards concentration around the mouth opening, has become lost altogether in the very degraded *Cestodes*, and is aggregated to form a pair of anteriorly placed ganglionic masses from which nerves stretch back along the sides of the body (see fig. 13, E), in the *Trematodes* and the higher *Turbellarians*. In the *Nemertean*s the same general arrangement is found, but the concentration is more complete and the anterior ganglionic masses are more definite. The two longitudinal nerves are long, and they are placed quite laterally. In some forms there is in addition, a certain amount of diffused nervous tissue in the body-wall, and in the walls of the proboscis. The *Palæonemertea* are the most nearly related to the primitive *Nemertean*s, while the *Schizonemertea* and the *Hoplonemertea* form two divergent series at the top of the branch.

The points of origin of the *Mollusca* and of the far-back ancestors of the *Vertebrata* from the *Vermes* were probably close together, and a little way above the origin of the *Platyelmia*. We can obtain a certain amount of information in regard to the probable ancestors of these higher groups of the *Metazoa* by comparing their larval forms. *Molluscan* larvæ may be referred to the same type as the *Trochosphere* (fig. 14), the typical larval form of the *Chætopoda* and some other groups of *Vermes* which will be discussed further on.

This larva is a bilaterally symmetrical body with a more or less rounded dorsal surface, which is prolonged anteriorly in front of the mouth as a præ-oral lobe. The alimentary canal is a slightly bent tube concave ventrally.* The mouth is ventral and the anus posterior, and the tube may be divided into three regions, the oesophagus, the stomach, and

* Compare with the primitive worm represented by fig. 13, E.

the rectum. A circle of long cilia is placed on the præoral lobe immediately in front of the mouth, and there may be also a perianal and several other post-oral bands of short cilia. There is often an epiblastic thickening of a nervous



Fig. 14. Trochosphere. *p*, præ-oral lobe; *q*, post-oral or abdominal part of body; *c*, præ-oral circle of large cilia; *p.c.*, perianal circle of cilia; *m*, mouth; *œ*, oesophagus (stomodæum); *s*, stomach; *i*, intestine; *a*, anus; *g*, supra-oesophageal ganglion; *o*, eye-spot.

nature in the præ-oral lobe, and simple sense organs may be developed in connection with it. Paired excretory organs may also be present in the form of small tubes opening to the exterior and communicating with the body cavity which surrounds the alimentary canal.

In the Echinodermata the typical larval form is characterised by having no ganglion or sense organs on the præ-oral lobe, and by the chief band of cilia being post-oral in position. In these respects it differs from the Trochosphere, and hence it has been argued* that the Echinodermata and the Mollusca cannot have had a common point of origin, but *Tornaria*, the larva of *Balanoglossus* (Enteropneusta), shows in some respects characters which are intermediate between those of the Echinoderm Bipinnaria larva and those of the Trochosphere. Balfour, however, has suggested that the resemblances of *Tornaria* to the Trochosphere are adaptive, and do not indicate close genetic affinity. If this should

* *Comp. Emb.* vol ii, p. 316.

turn out to be the case, the common origin of the Chordata, the Enteropneusta, and the Echinodermata (for these three groups are undoubtedly related) must be moved back on the main axis so as to be at a different point from the origin of the Mollusca, and nearer to the Gastrea.*

Turning now to the branch representing the phylum Mollusca† we find that no existing forms are very primitive. Probably the most nearly related to the ancestral Molluscs are those composing the group Isopleura, but even they are very considerably differentiated. To express this a long line has been left between the origin of the Molluscan branch and the first point of division into the ancestral forms of the existing groups of the Mollusca.

Professor Ray Lankester has reconstructed the probable common ancestor of the Mollusca, the form which occupied the point of division of the branch into primitive Isopleura, Lamellibranchiata, and Cephalophora. This Archi-Mollusc (fig. 15) is bilaterally symmetrical and elongated antero-posteriorly. It has a flat ventral and a rounded dorsal surface. The head is well marked, and has a region in front of the mouth (prostomium) on the upper surface of which are placed a pair of cephalic tentacles. The mouth is placed in the middle line anteriorly, but behind the prostomium. The anus is placed in the middle line posteriorly, and rather on the dorsal surface. A pair of renal excretory organs (nephridia) open one at each side of the anus, while close to the nephridial apertures, but further forward, are the openings of the paired reproductive organs. The ventral surface of the body is formed of a thick muscular

* Balfour advocates the view that the Echinodermata at least have sprung from a radially symmetrical ancestor, and that the bilateral symmetry of the larval forms is secondary (*Comp. Emb.*, vol. ii, p. 318.)

† The student is referred to Lankester's article "Mollusca," *Ency. Brit.* 9th ed., p. 632.

mass extending from behind the mouth backwards to the posterior end of the body. This is the characteristic molluscan "foot." (Fig. 15, A).

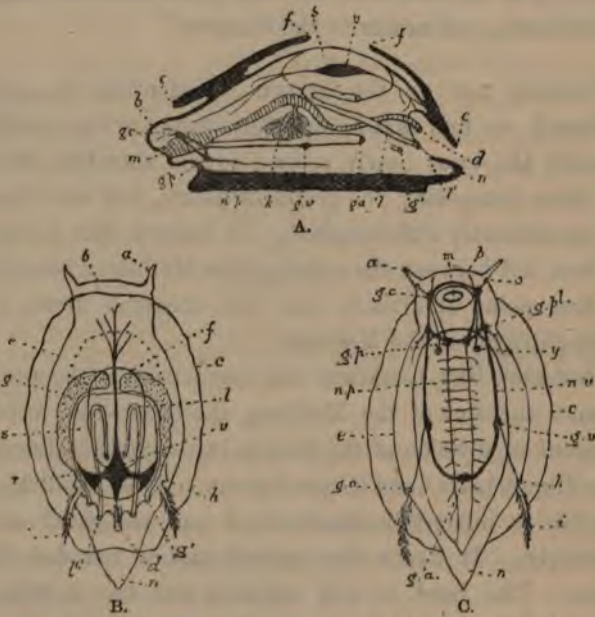


Fig. 15. Archi-Mollusc. Three diagrammatic views taken from Lankester's figures. A, Vertical antero-posterior section. B, Dorsal view, in which the body-wall is supposed to be transparent, allowing the circulatory, renal, reproductive, and other organs to be seen through. C. Ventral view shewing the nervous system. *a*, cephalic tentacle; *b*, head; *c*, free edge of mantle skirt; *d*, anus; *e*, edge of the foot; *f*, edge of the shell follicle; *g*, gonad, or reproductive organ; *g'*, opening of duct from gonad; *h*, osphradium; *i*, ctenidium; *k*, liver; *l*, nephridium; *l'*, opening of nephridium; *m*, mouth; *n*, posterior end of foot; *o*, cephalic eye; *r*, auricle of heart; *s*, pericardium; *v*, ventricle of heart, giving off an anterior and a posterior vessel; *y*, otocyst; *g.a.*, abdominal ganglion; *g.c.*, cerebral ganglion; *g.o.*, olfactory ganglion; *g.p.*, pedal ganglion; *g.pl.*, pleural ganglion; *g.v.*, visceral ganglion; *n.p.*, pedal nerve; *n.v.*, visceral nerve.

Covering the rounded dorsal surface (the "visceral dome") is a cap-shaped shell, which is exposed in the centre but has its edge all round embedded in a flattened sac in the body-wall—the primary shell follicle (fig. 15, A and B). On the edge of the visceral dome the wall of the body

projects all round in the form of a flap (the mantle skirt) overhanging the head and the sides of the foot. The space between the mantle skirt and the sides of the body is the subpallial chamber, and into this the anus and the nephridia and generative apertures open. From each side of the body, rather far back, there grows out into the subpallial chamber a process of the body-wall, consisting of an axis (containing two blood vessels) from which a double row of filaments hang down. These organs are the gills or ctenidia (fig. 15, B and C). Near the base of the ctenidium on the body-wall there is a sense organ (the osphradium) composed of modified epithelium and having a special ganglion and nerve in connection with it. Its probable use is to test the quality of the water flowing over the gills.

The mouth leads into the stomodæum, an anterior portion of the alimentary canal which is epiblastic in origin, and which forms a muscular bulb. At the posterior end of the intestine there is a short proctodæum, which is also derived from the epiblast. The alimentary canal between these two terminal parts is the remains of the archenteron and is therefore hypoblastic. An outgrowth from this region on each side forms the liver. Around the alimentary canal is a cavity (the cœlom), which has been formed from diverticula of the archenteron, corresponding probably to the intermesenteric spaces in the Actinozoa, and in which the blood flows. The cœlom is more or less broken up into small spaces, but a large open region is found dorsally to the alimentary canal, and in this (the pericardium) lies a muscular tube, the heart, which propels the blood through ill-defined vessels and lacunæ, which are merely parts of the cœlom. The heart consists of two lateral dilated thin-walled sacs, the auricles, which receive the purified blood brought back from the gills and pour it into the median thick-walled muscular tube, the ventricle, which on contracting drives the blood out through

two terminal vessels, the anterior and posterior aortæ. The nephridia are coiled tubes which open by one end into the pericardium (cœlom), and by the other to the exterior, close to the anus.

The nervous system of the *Archi-Mollusc* is rather complicated and consists of eleven ganglia and various connecting nerve-cords (see fig. 15. C). There are two cerebral ganglia above and in front of the mouth, and connected by the cerebral nerve commissure. At each side of the stomodæum is a pleural ganglion, and below it a pair of pedal ganglia. The two pleurals and the two pedals are connected below the stomodæum by a commissure, and each ganglion is connected also with the cerebral of its own side. From each pleural ganglion a visceral nerve is continued backwards below the alimentary canal to a visceral ganglion from which a nerve is given off to the small ganglion connected with the osphradium at the base of the gill. The two visceral ganglia are joined posteriorly by a visceral loop in the middle of which, below the intestine, a median abdominal ganglion is placed. Finally each pedal ganglion is united to the pleural of its own side and gives off also a posteriorly directed nerve which runs backwards along the lateral part of the foot. A pair of auditory organs (the otocysts) are placed in the front of the foot, and an eye-spot is present at the base of each cephalic tentacle.

From such an ancestral form as this* all the existing groups of *Mollusca* have probably been derived. The descendants of the *Archi-Mollusc* must have split into two great divergent series which have resulted in the production of the *Lamellibranchiata* on the one hand, and the *Cephalophora* on the other.

In the first of these ancestral lines, the primitive Mol-

* For further details see Ray Lankester's article, "*Mollusca*," *Ency. Brit.*, 9th ed., p. 635.

luscan characteristics have been modified as the result of a more or less stationary mode of life. The head region, including the prostomium, the cephalic tentacles, and the eyes, has become more and more rudimentary so as to be finally suppressed altogether. The primitive bilateral symmetry is retained, but the body is much compressed from side to side, the result being that the foot is either nearly aborted or is reduced to a narrow projection. In consequence of the flattening, the mantle is also changed and takes the form of two large laterally placed lobes, on the outer surface of each of which a valve or plate of the shell is formed. The ctenidia have become enormously enlarged to form two great gill-lamellæ on each side of the body. Besides being respiratory in function, they also, by their extended ciliated surface, cause currents of water which bring food particles to the mouth—an important matter to an animal with very limited powers of movement. The cerebral, pleural, and visceral ganglia of each side of the body have coalesced to form a single mass, the so-called cerebral ganglion, placed alongside the mouth. The pedal ganglia are normal, and the osphradial are very large and are usually known as parieto-splanchnic. Two large muscles run transversely across the body, one in front of and above the mouth, and the other below the anus. They serve to approximate the valves of the shell, and are the anterior and posterior adductor muscles.

In the primitive Lamellibranchs, these muscles were probably of much the same size, and we find the most direct descendants of such forms in the Isomya of the present day, and especially in the Integropalliata, such as *Arca*, *Nucula*, and *Trigonia*, which may be regarded as being more in the direct line of development than any of the other Lamellibranchiata. From this stock two divergent lines have sprung. On the one hand, the Sinupalliata have

been evolved upwards; and on the other, the *Heteromya* and the *Monomya* have degenerated.

The *Sinupalliate* have remained *Isomya*, both adductors being well developed, but the posterior parts of their mantle lobes have become prolonged and united to form a pair of siphons through which the water flows into and out of the pallial cavity, and the line of attachment of the mantle to the shell has been inflected so as to form a sinus into which the siphons may be more or less completely withdrawn.

In the other series we have, starting from one of the primitive *Integropalliate Isomya*, the anterior adductor muscle becoming more and more reduced so as to produce first the *Heteromya*, including such forms as *Mytilus*, where the muscles are very unequal in size, and then the *Monomya* (*Ostrea*, *Anomia*, *Pecten*, &c.), where the anterior adductor is entirely absent. That the *Monomya* have really degenerated from *Isomya* is very clearly proved by Huxley's discovery that the oyster (*Ostrea*) when very young has both adductors well developed, but loses the anterior one later on, thus recapitulating in its development the ancestral history. The various groups of *Lamellibranchiata* differ from one another also in the structure of the gill-lamellæ, which may become very complex, and in the special development of the pallial siphons and the foot.

In the second ancestral line, starting from the *Archimollusc*, the prostomial region has been retained and developed into a well-marked head with cephalic sense organs, and a special and very remarkable organ, the odontophore, has been developed in connection with the stomodæum. This organ consists essentially of a band, covered by transverse rows of chitinous teeth, stretched over a cartilaginous mass placed on the floor of the buccal cavity, and capable of being protracted and retracted by special

muscles.* From this ancestral Cephaloporous or Glosso-phorous Mollusc, which is continued up into the primitive Gastropoda, two lines have diverged. The first, with comparatively little modification, to the Isopleura, and the second, with a considerable amount of divergence, to the Scaphopoda.

In the Isopleura, the primitive bilateral symmetry has been retained, and most of the systems remain very much in the condition in which they were found in the Archi-Mollusc, with, of course, the addition of the odontophore. The Isopleura include three groups:—the Polyplacophora, or Chitons, in which the simple dorsal shell has been multiplied so as to form a series of eight valves; and the Neomeniæ and Chaetoderma in which the shell is represented by numerous minute calcareous plates or spines, and the mantle and foot are much reduced, and the body is worm-like in form. These are the most primitive Gastropodous Molluscs which are known.

The Scaphopoda (*Dentalium*) are much more modified, and possibly somewhat degenerate. They have retained the primitive bilateral symmetry, but the body has become greatly elongated antero-posteriorly, and the foot is especially produced anteriorly, and adapted for burrowing in sand. The mantle-skirts have fused ventrally below the foot, so as to produce a cylindrical body-form, and around this the shell is developed as a cylindrical tube, open at both ends. The heart seems to have been lost during the stages which have intervened since the Scaphopoda diverged from the primitive Gastropods.

Returning to the line leading upwards to the higher Cephaloporous Molluscs, we find that after the ancestral Scaphopoda had diverged, the visceral dome must have increased greatly in size, so as to form a great dorsal pro-

* For a description, with figures, of the odontophore, see Lankester's article, "Mollusca," *Ency. Brit.*, 9th edition, p. 640.

jection, containing the greater part of the digestive and reproductive viscera. Then two great lines of descent were produced, one leading to the Pteropoda and Cephalopoda, the other to the Gastropoda.

Following up the last of these we find that a large shell became developed as a protection to the visceral mass, and that (possibly, as Lankester suggests, as a result of the weight of the shell falling on one side) the visceral dome became twisted round spirally to the right, so that the anus which was originally posterior came to be placed first on the right side of the body, and then anteriorly above the head. The whole visceral mass has also in most cases come to be more or less coiled spirally, and the shell covering it has taken the same form. By these changes the bilateral symmetry was entirely destroyed. The ctenidia and the nephridia and other paired organs shared in the torsion of the visceral mass, and, in most cases, became unequally developed on the two sides in consequence. In many cases the ctenidium and nephridium, which were originally on the left side of the anus, and which, after the changes, came to be upon the right side, have become atrophied.

There is reason to believe that these ancestral Gastropods split into two series, in the one of which the visceral nerve loop, with the visceral ganglia, became implicated in the rotation of the visceral mass, the result being that the loop was twisted into a figure of eight, and the ganglia changed sides; while in the other series, possibly on account of the deeper position of the nerves in the body, they were not affected by the other changes. For the first of these series, in which the nerves cross, Spengel has proposed the name *Streptoneura*; and for the second, in which the visceral nerves remain straight and unaltered, *Euthyneura*.

The primitive *Streptoneura* divided into two series: the *Zygobranchiata* (*Patella*, *Haliotis*, &c.) in which the

ctenidium and nephridium on the right side of the body did not atrophy, but are as large, and sometimes larger, than those on the left side; and the Azygobranchiata, in which the ctenidium and nephridium on the right side of the body have been lost. This last is a very large group, including the majority of the Gastropoda, and is considerably more modified than the Zygobranchiata.

The Heteropoda are a divergent group of the Streptoneura. They agree with the Azygobranchiata in their essential characters, but have become adapted to a free-swimming existence. The foot is especially modified in some forms (*e.g.*, *Carinaria*) into a flattened fin-like organ, provided with a sucker. The visceral mass may become greatly reduced, and the shell may be entirely lost.

The Euthyneura are characterised by their straight visceral nerves, and by the atrophy of the paired organs on the right side of the body. They are all hermaphrodite, and in many cases the shell is absent. The ancestral Euthyneura are represented by the Opisthobranchiata of the present time, including two series, the Nudibranchiata and the Tectibranchiata; while the Pulmonata are a divergent group, derived from the primitive Opisthobranchiata. In the Opisthobranchiata the heart is placed anteriorly to the base of the gill. In the Nudibranchiata the mantle-skirt and the shell are both absent. Some extraordinarily modified forms belong to this latter group. In many the ctenidium is absent, and respiration is performed by other processes from the body wall.

The Pulmonata have become adapted to a terrestrial life. The ctenidium has been lost, and the pallial cavity has become converted into a respiratory sac, communicating with the exterior by a small aperture. In some forms (*Limax*, &c., the slugs) the visceral mass is greatly reduced, and the shell is either very small or altogether absent.

Returning now to the primitive Cephalophora, after the ancestors of the Scaphopoda had diverged, we must trace the line leading up to the Cephalopoda and the Pteropoda. In this series the primitive bilateral symmetry has been retained, and the visceral mass has been greatly enlarged, so as to produce a great dorsal projection, but no twisting of this region takes place, the anus remaining in its primitive posterior position. The foot has been greatly modified, in accordance with the free-swimming habits of the animals. Its front part has grown upwards and forward, so as to surround the head, the result being that the mouth is placed in the anterior portion of the foot, and opens ventrally. In most cases this region of the foot is drawn out radially into paired processes, which may be provided with suckers. The median part behind the head is developed into a pair of flaps (the epipodia), which may be used as swimming organs, or modified to form a posteriorly placed funnel. The remainder of the foot is undeveloped. A shell, if present, is light and fragile.

Such an ancestral form as this is most nearly represented at the present day by the Pteropoda, a group which diverged far back, and probably have undergone comparatively little modification. Some of them are probably degenerate. The epipodia have remained in their primitive condition as large muscular flaps, and are used as swimming paddles. The other parts of the foot may remain in a rudimentary condition. The ctenidia have been lost, and in one section of the group (the Thecosomata), where a mantle and shell are present, the walls of the large subpallial cavity act as organs of respiration. In the Gymnosomata the mantle skirt is absent, and there is no shell.

The ancestral Cephalopoda, after the Pteropoda had diverged, must have had their epipodia modified, so as to become more or less completely united in the middle line

posteriorly, to form a tube (the siphon or funnel), open at both ends, which would serve to conduct the water outwards from the subpallial chamber. The front of the foot, surrounding the mouth, must have become well developed, and drawn out on each side into four or five projections. The other systems remained in their primitive typical condition.

This ancestral line divided into two branches, the one leading to the Tetrabranchiata (*Nautilus* and extinct forms, e.g., Ammonites), and the other, after a considerable amount of further evolution, to the Dibranchiata, including the ordinary cuttlefishes. The Tetrabranchiata possess two pairs of ctenidia and two pairs of nephridia, and the epipodia are not completely united. The lobes of the front part of the foot bear numerous tentacular processes, but no suckers. A large external shell, divided into a series of chambers, is present.

The ancestral Dibranchiata after separation from the Tetrabranchiata must have undergone some further changes. The fusion of the epipodia became complete. The lobes of the fore-foot developed rows of suckers (acetabula), and the shell became enclosed in folds of the mantle so as to be internal. The nervous system and sense organs became more highly evolved, and finally, an "ink" sac was developed. The Dibranchiata are divided into two groups (Octopoda and Decapoda) according to the number of processes developed from the foot surrounding the mouth. The very long line occupied by the series of ancestral Cephalopoda indicates the extensive modifications the group has undergone during its evolution. The Dibranchiata occupy the highest point in the Mollusca and are very far above the place of origin of the phylum from the Vermes. This shows the great range of organisation which is found amongst the Mollusca.

The Echinodermata, it has already been seen, probably

arose along with the Enteropneusta and the early Chordata by a common root from the Vermes, close to the point of origin of the primitive Mollusca, or possibly a little further back. This branch is the largest and most important in the table. It probably very soon broke up into two series of ancestral forms; (1) those which lead upwards to the Vertebrata, and to which we shall return later on; and (2), the common ancestors of the Enteropneusta and Echinodermata. This latter series is now represented by *Balanoglossus*, which may be regarded as the termination of the primary branch having as lateral off-shoots the Echinodermata on the one hand, and the Proto-Chordata on the other.

The relationship between the Echinodermata and the Enteropneusta is shown by *Tornaria*, the larva of *Balanoglossus* agreeing with the typical Echinoderm larva in all its most important characteristics.* The ancestral forms of this branch may be regarded as being derived from the Trochosphere (or possibly from a rather more generalised form which had not yet acquired all the special Trochosphere characters), after separating from which, they must have acquired such peculiar features as the longitudinal post-oral band of cilia, and the derivation of a water-vascular system from the archenteron. From such an ancestor *Balanoglossus* has probably been derived very much as we see it developing at the present day from the *Tornaria* stage, by the disappearance of the longitudinal band of cilia, the conversion of the præ-oral lobe into the proboscis, the elongation of the body into a worm-like form, and other changes.

The line along which the Echinodermata were evolved is not so easy to trace. Probably their first ancestors (fig. 16) differed from the ancestors of the Enteropneusta in that portion of the cœlom (diverticula from the archenteron), which formed the water-vascular system being developed

* See Balfour, *Comp. Embryol.*, vol. i, p. 485.

radially, or as a series of pouches around the front part of the alimentary canal, so as to produce the first traces of the more or less complete radial symmetry which is such a marked feature in all Echinoderms. If the nervous system was still in its primitive diffused condition, it may readily be imagined that the formation of radially arranged regions of the coelom, which were being evolved into vessels with tentacle-like projections to the exterior, would result in the concentration of the nervous tissue along these lines; and if, as is probable, there was previously a nervous concentration around the mouth, then the newly formed nerve bands would naturally radiate outwards from the circum-oral ring (see fig. 16). The other characters which the common

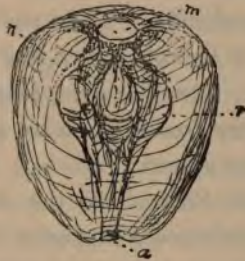


Fig. 16. Hypothetical ancestor of the Echinodermata. *m*, mouth; *a*, anus; *n*, nerve cord; *r*, water-vascular diverticulum from archenteron.

ancestor of the Echinodermata must have acquired are:—a tendency towards the formation of the water-vascular caeca in fives, and as a result the pentagonal symmetry of most of the systems of the body; the development of a large coelom or body cavity; and the deposition of calcareous matter in the deeper parts of the integument.

The ancestral line then probably split into two series:—the one being continued into the progenitors of the Asteroids, the Ophiuroids, and the Crinoids, and the other being evolved into the primitive Echinoids and Holothurians.

In the latter series the primitive body-form was most nearly retained, but all the systems became considerably differentiated.

In the ancestral Holothuroidea the shape became elongated antero-posteriorly, and, as a result, the pentagonal arrangement of many of the parts was masked. The calcareous deposits in the integument remained as scattered spicules, while strong bands of muscle were developed to strengthen the body wall. At the anterior end, around the mouth, a part of the water-vascular system was prolonged outwards to form a series of large tentacles, while at the posterior end of the body a pair of large branched tubular organs (the "respiratory trees") in all probability place the coelom in communication with the exterior through the cloaca, and act as nephridia. From such an ancestral form the various groups of Holothuroidea may be readily derived. Some of them (*e.g.*, *Synapta*) are probably slightly degenerate, the respiratory trees and some parts of the water-vascular system being absent.

In the ancestral Echinoidea the body became more globular, and the calcareous deposits in the integument were increased greatly, so as to form eventually a continuous shell composed of regularly arranged plates, and bearing spines and other calcareous projections on its outer surface. Some of the existing groups of Echinoids have become highly differentiated, but all the systems may be traced back to those of the ancestral form. The water-vascular system has become an important and complicated series of organs, and a very elaborate calcareous apparatus, bearing teeth (Aristotle's lantern), has been evolved in connection with the mouth.

Returning now to the main branch of the Echinodermata, and tracing it onwards towards the Asteroidea, Ophiuroidea and Crinoidea, we find that in the common ancestors of

these groups the body form must have become considerably changed. It must have been flattened antero-posteriorly, so as to reduce the oro-anal axis, and then pushed out radially along the lines of the chief parts of the water-vascular system, so as to produce, first a pentagonal, and then a stellate shape. There being then only half the body in a position for creeping, the water-vascular system was developed only on the lower (oral) surface, in place of extending almost to the aboral pole, as in *Holothurians* and *Echinoids*.

From such an ancestor the *Asteroidea* were probably given off, and they have retained all the essential characters, while some of their systems have become more highly differentiated. In the *Ophiuroidea* and the *Crinoidea* the radial processes of the body or arms have become more marked, and the formation of calcareous matter has increased greatly, the result being that the arms are almost entirely solid, and in great part formed of calcareous ossicles. These changes took place after the separation of the ancestral *Asteroids*, so that probably the *Ophiuroids* and *Crinoids* have had a rather longer common ancestry.

The ancestral *Crinoids*, after the *Ophiuroids* diverged, then probably became fixed by the aboral end of the body, and this necessitated a change in the position of the anus, resulting in both openings of the alimentary canal coming to lie upon the same surface of the body. The extinct *Cystoidea* and *Blastoidea* may be placed as neighbouring side branches from the primitive *Crinoids*. Probably these three groups are all somewhat degenerate.

The remarkable characteristics acquired by most *Echinoderms* during their larval stages (*e.g.*, *Pluteus*) are certainly merely adaptive and have no phylogenetic significance, and this explains the sudden, and in some cases, very profound changes which may take place when the animal throws off its temporary larval characteristics and acquires its adult structure.

Returning to the main stem of the table, we find a number of comparatively small groups, lying between the primitive Echinoderms and the higher worms, which are probably all derived from side branches given off from what may be called the middle third of the vermean axis—the lower third being the region below the point of origin of the Mollusca, and the upper third above the origin of the Arthropoda. These small groups are all rather aberrant, and some of them are certainly degraded.

The Nematelmin worms are represented by a branch extending upwards to the right above the common origin of the Chordata and the Echinodermata. The members of this group are less unlike the typical Vermes than is the case with most of the other branches from the middle third of the vermean axis. The highest forms of the group are the Nematoda, while the Acanthocephala (*Echinorhynchus*) must be regarded as a degraded offshoot, sloping downwards from near the base of the Nematelmin branch. The degeneration of *Echinorhynchus*, and probably of some of the Nematoda also, is a result of their parasitic mode of life.

The Gephyrea have probably arisen from the main stem, not far from the point of origin of the Nematelmia. They have developed a spacious cœlom, and in most cases a long convoluted alimentary canal. On the other hand, they retain the characters of primitive Vermes in the absence of true segmentation, and in the larval præ-oral lobe developing into an important part of the front of the body. In most, a small number of paired nephridia are present, and in some cases (*e.g.*, *Bonellia*), two of these placed at the posterior end of the body become greatly enlarged to form branched organs, placing the cœlom in communication with the proctodæum, as in the case of the respiratory trees in the Holothuroidea.

The affinities of the Brachiopoda are still unsettled. The larvæ of some forms (*e.g.*, *Argiope*) appear to shew close

relationship with the Chætopoda, but there is a want of agreement between the groups in some points which makes the matter doubtful, and therefore it is safer at present not to regard the Brachiopods as degraded Chætopoda, but as derived from a lower point in the vermean series. The exact position of that point of origin is very doubtful; probably it lay above the primitive Gephyrea, but below the origin of the Rotifera. The present Brachiopods must be regarded as having degenerated in accordance with their sessile mode of life.

The Polyzoa are also degenerate forms belonging in all probability to this division of the Vermes. The larvæ are free-swimming ciliated forms, which may be compared with the Trochosphere stage found in the development of so many Vermes. Balfour* regards them as Trochospheres, which became fixed in the adult by the extremity of the præ-oral lobe. He also shows that there is reason to consider the Polyzoa as exhibiting alternation of generations. The ovum develops into a free-swimming form (the so-called larva), which never becomes sexual, but produces by budding the attached form (the adult Polyzoön), which develops reproductive organs. From the fact that Cyphonautes, the larva of *Membranipora*, an ectoproctous Polyzoön, is itself entoproctous, it is probable that the Entoprocta (*Pedicellina*) are more primitive than the Ectoprocta. Both groups are, however, degenerate and considerably modified.

The Chætognatha (*Sagitta*) are a small group with obscure affinities, which are best placed in this part of the vermean series close to the origin of the Arthropoda. Possibly they may be more closely related to the Nematelmia than is shown by the table.

The Rotifera are certainly degraded, but what they have been derived from is somewhat doubtful. *Pedalion* appears

* *Comp. Embryol.*, v. i, p. 255.

to show Arthropod affinities in some of its characters, and it is possible that the group may be connected with the base of the Crustacean series. On the other hand, the Rotifera retain in the trochal disc an organ which is apparently the ciliated præ-oral lobe of the larvæ of so many of the Vermes, and this seems to shew that they have arisen directly from the vermean axis. Some of the groups of Rotifera have degenerated to a very great extent.

We now come to the important region where the two great Arthropodan series, the Crustacea and the Tracheata, diverged from the base of the higher worms at or about the same point. It is probable, from a consideration both of the anatomy and of the development of the two groups, that they do not belong to one great series, but have been evolved independently, and therefore, having no common ancestors nearer than the Vermes, they must have acquired separately such Arthropodan characteristics as they possess in common. The Tracheata are descended from some primitive Annelidan form allied to *Peripatus*, while the Crustacea must have had as their common ancestor a primitive Phyllopod, and the differences between these two types—*Peripatus* and the Phyllopod—are so great that they cannot have had any common ancestry nearer than the Vermes. The similarity of some of the organs in the two series may be explained by considering them as similar differentiations of parts inherited from their Annelidan ancestors, while other common characteristics may be regarded as being merely adaptive, and due, in some cases, to similar modes of life and habits.

At the point where the Crustacea and Tracheata diverge the Vermes must have already acquired some of the characteristics of their higher groups, such as true segmentation, or the formation of metameres; and rudimentary appendages, as simple processes developed in pairs, one from

each metamere. Renal organs were present in the form of paired nephridia. In the ancestral Crustacean, derived from this primitive segmented worm, the lateral appendages must have become developed into more efficient locomotory organs, by their elongation and the formation of joints upon them. The increased power of movement which this change conferred probably resulted in an increase in the muscular system connected with the appendages, and this, in order that the new organs might be fully taken advantage of, would require the formation of a hard skeletal tissue, to which the muscles might be attached. To meet this want, the more or less calcified cuticular "shell" of the Crustacea was developed, and, in the higher members of the group, has been brought to a high degree of perfection as an exoskeleton.

The further changes which have taken place during the evolution of the Crustacea, have been mainly in the direction of producing "heteronomy" in the segments of the body. Division of labour amongst the appendages has resulted in great modifications in structure, some being converted into jaws, others into sense organs, walking legs, swimming legs, and other organs; while the segments themselves have also undergone change, the exoskeleton becoming in many cases fused over large tracts to form a continuous hard covering or carapace. Some of the metameres at the front of the body more or less completely unite with the præ-oral lobe to form a distinct "head."

The free larval stage known as the Nauplius, is of such constant occurrence throughout the Crustacea, though exhibiting slight peculiarities in each group, that it is almost certain that it represents more or less closely a far-back common ancestor. The Nauplius of the Phyllopoda (fig. 17), the most nearly primitive group of Crustaceans, is an ovate body, provided with three pairs of appendages, attached to the anterior (cephalic) region. These appendages afterwards

become the two pairs of antennæ and the mandibles. The first pair of antennæ are comparatively slight, consist of one



Fig. 17. Phyllopod Nauplius (*Apus*) when hatched (after Claus). 1, first pair of antennæ; 2, second pair of antennæ; 3, mandibles; l, labrum; o, median eye; s, segments of the post-cephalic region of the body.

branch only, and are probably sensory organs. Between their bases is placed a large upper lip or labrum, behind which lies the mouth. The second antennæ are very much larger, and are biramous, with a spine projecting from near the base inwards towards the mouth. These appendages are the main organs of locomotion of the Nauplius. The mandibles are rather smaller. They represent the mandibular palps of the adult, and are biramous. On the front of the head is placed a median unpaired eye. The post-cephalic region shews traces of five segments and their appendages, and in this respect differs from most Nauplii, which are unsegmented.

Probably this Phyllopod Nauplius is the nearest form known to the primitive Crustacean, but it must remain doubtful whether or not additional post-cephalic segments with simple biramous appendages were present. From this form the existing group of Phyllopoda was probably evolved very much as we find *Apus* developing from the Nauplius stage at the present day. The modifications of form and structure take place gradually, without any sudden metamorphosis. This ancestral series of Proto-Phyllopods has formed the main axis of the Crustacean branch from which the various existing groups have been

given off at different points. It ends in the existing Phyllopoda, the nearly allied Cladocera being shown as a slightly divergent side branch.

The Copepoda, the Cirripedia, and the Ostracoda have all probably arisen independently from the ancestral stem, and have become considerably modified in different directions. The Copepoda are probably the oldest group. They retain the median Nauplius eye and have simple biramous appendages. A number of the Copepoda are certainly degenerate forms, and some of them are very much modified.

The Cirripedia probably arose further up the main stem, and in the ancestral condition were characterised by the possession of a large carapace, in the form of a bivalve shell. We see the remains of this stage in the "Cypris" larva of existing Cirripedes. The group has undergone very great modifications since, due doubtless to the change from a free-swimming to a sessile existence. A considerable amount of degeneration has also taken place amongst the Cirripedia.

The Ostracoda probably arose from a point still further up in the series of the Proto-Phyllopods, and have undergone a good deal of modification. A bivalve shell has been developed to such an extent as to enclose the entire body. In some members of the group degeneration resulting in the loss of the heart and the compound eyes has taken place.

The higher Crustacea have arisen from the main axis of the group, below the point of separation of the Cladocera from the Phyllopoda, but probably not much further back, and the Nebaliadæ are, according to Claus,* the nearest forms we know to the primitive Malacostraca. Possibly after this, as suggested by Balfour,† the thoracic appendage

* *Ueber den Bau und die systematische Stellung von Nebalia. Zeitsch. f. Wiss., Zool.*, Bd. xxii (1872).

† See Balfour, *Comp. Embryol.*, vol. i, p. 420.

became reduced, and a form was assumed which is more or less nearly represented by the Zoëa stage, which occurs in the development of most of the higher Crustacea.

The Edriophthalmata must have sprung from the primitive Malacostraca far back. They have no Zoëa stage, and consequently may have diverged during that first Phyllopod condition of the Malacostraca which *Nebalia* still represents, or they may have arisen later on and have lost the Zoëa stage in their development since. The Edriophthalmata probably underwent a considerable amount of divergence before breaking up into the groups now existing. The Stomatopoda and Cumacea may be represented as short lateral branches from the Malacostraca after the Zoëa-like ancestral stage. The Cumacea in some respects show resemblances to the Edriophthalmata.

The ancestral Podophthalmata then split into the Schizopoda, a small group which did not diverge much, and which may be taken as representing an ancestral stage (*Mysis*), and the Decapoda, which after some further evolution, including the loss of the Schizopod character—the presence of exopodites on the posterior thoracic appendages—became broken up into the ancestral forms of the existing groups. The Macrura and the Brachyura form two somewhat divergent series, while the Anomoura have undergone considerable modification or degeneration. *Penæus*, amongst the Macrura, has been shown by Fritz Müller* to leave the egg as a Nauplius, and to go through a series of larval stages, which probably represent more nearly than any other forms the more important ancestral stages in the phylogeny of the Crustacea.

In the Decapoda the evolution of the sense organs, the efficiency of the exoskeleton, the heteronomy of the segments, and the specialization of the appendages reach their highest degree of perfection.

* *Facts for Darwin*, London, 1869.

Recent researches* on the structure and embryology of *Peripatus* (Onychophora in table) have shown that while it is distinctly one of the Tracheata, in as much as it possesses respiratory organs in the form of tracheæ, it still exhibits the Annelidan feature of paired nephridia corresponding to the somites. *Peripatus* from its geographical distribution must be regarded as a very ancient type, and in all probability it represents the ancestral Tracheata close to the point of their divergence from the Vermes. It has probably become slightly modified by degeneration, but still is extremely useful in helping us to form an idea of the series of changes by which the Tracheata were evolved. The ancestral worm from which the branch started must be regarded as having attained about the same level of high organisation as the form from which the series of Crustacea arose, consequently the two great Arthropodan branches may have diverged from a common ancestor in the Vermes.

The primitive Tracheata had an elongated worm-like body, which was divided into segments, probably with comparatively little heteronomy. Each segment was prolonged laterally into a pair of processes, the appendages, which were beginning to be transversely segmented or jointed. The muscular system was becoming more highly differentiated, and the cuticle had partially hardened to form an exoskeleton. The characteristic excretory organs of the Vermes were still retained in the form of laterally placed nephridia, a pair in each segment; but the typical respiratory system of the Tracheata had commenced to develop, probably at first as a series of slight ectodermal depressions which gradually worked their way deeper and deeper into the tissues until they formed a system of tubes, branching through the body

* Moseley on the Structure and Development of *Peripatus capensis*, *Phil. Trans.*, v. 164 (1874); and Balfour, *Quart. Jour. Micros. Sc.*, vol. xix (1879) and vol. xxiii, no. xc, p. 213 (1883).

and lined by a delicate chitinous cuticle. The appendages at the front of the body were beginning to be specialised in connection with the head and mouth opening, the first pair becoming elongated as sensory antennæ, and the three following pairs being modified into jaws.

It is such an ancestral form as this (Proto-Tracheata) that *Peripatus* represents, and that was continued upwards to the primitive Myriapoda. Above the ancestral stage perpetuated by *Peripatus* the nephridia were lost, and the segmentation of the appendages and the formation of the tracheæ became more perfect. The Myriapoda have remained in very much this condition, the body being still formed of a large number of segments showing very little heteronomy.

From the ancestral Myriapoda the line leading to higher Tracheata diverged and may be traced upwards to the base of the series of Arachnida and Insecta. Near to the ancestral Arachnida may be placed a few aberrant groups with somewhat doubtful affinities. Of these the most distinct is the Pantopoda (Pycnogonida), a class* which is not closely allied to any of the neighbouring groups, and is best regarded as forming a branch by itself which has diverged from the line leading upwards from the Proto-Tracheata and Myriapoda. In the Pantopoda the number of segments in the body has become greatly reduced, the posterior ones (those forming the abdomen in higher Tracheata) being in a rudimentary condition. The appendages have become enormously elongated, and those around the mouth considerably modified. The tracheæ have been altogether lost.

The Tardigrada and the Pentastomida are more closely allied to the lower Arachnids than to the Insects, and were probably divergent and degenerate off-shoots from the

* See Hoek, *Challenger Zoological Reports*, vol. iii, part x, "The Pycnogonida," p. 145.

ancestral Arachnida. The extinct Trilobites were possibly derived from this part of the Tracheate series, while the Pœcilopoda* (*Limulus*), and their ancestral allies the Eurypterida form a branch probably from this region of the primitive Arachnida.

From about the same point must have diverged the ancestral series leading upwards to the higher Arachnida. Of these the Arthrogastra (*Scorpio*) are probably the most nearly in the direct line of development, while the Araneina and the Acarida are two divergent and more modified series. The Acarida are probably somewhat degenerate, and the Araneina are the most highly differentiated group in this branch of the Tracheata. In these higher Arachnids pulmonary sacs to a large extent replace tracheæ as respiratory organs.

At the point where the ancestral Insecta (Hexapoda) diverged from the primitive Arachnida and Pantopoda, the number of segments in the body must have become restricted to about seventeen or eighteen, and were arranged in three groups—four constituting the head, three the thorax, and ten or eleven the abdomen. At first these segments were provided each with a pair of appendages, and the Thysanura and Collembola (constituting together the Aptera of the table) may be regarded as the degenerate representatives of such a stage. They are decidedly the most nearly related of all Insects to the primitive wingless ancestors,† and retain, along with other ancestral characters, rudiments of abdominal appendages (*Campodea*).

Above the point where the Aptera diverged, certain important changes must have taken place. The abdominal

* See Ray Lankester, *Limulus an Arachnid*, *Quart. Journ. Micros. Sc.*, vol. xxi, Nos. lxxxiii and lxxxiv. (1881).

† See Lubbock, *Monograph on Collembola and Thysanura*, Ray Society, 1873; and Balfour, *Comp. Embryol.*, vol. i, p. 353.

appendages were lost, and those of the thoracic region alone remain as the three pairs of legs characteristic of the Insecta. Wings then developed, as outgrowths from the dorsal region of the second and third thoracic segments, one pair on each. The Orthoptera most nearly represent this ancestral stage. They are certainly more primitive than any of the higher orders of Insects, and probably, along with their allies, the Neuroptera, the Pseudo-Neuroptera, and the Dermatoptera (forming altogether Packard's "Phyloptera" *), constitute a branch which diverged about this point.

Higher up, the main stem probably split into two branches, one leading through the ancestral Hemiptera, after considerable modification, to the Coleoptera, † while the other forms the line from which the ancestral Diptera, Lepidoptera, and Hymenoptera successively diverged. Some of the Diptera have undergone considerable degeneration. The Hymenoptera are the most perfectly differentiated forms. They attain to a higher level of organisation than any of the other Tracheata, and probably occupy the highest point among Invertebrates. The Insecta is a very extensive class, but, notwithstanding the very large number of species it includes, and the high position attained by some of its members, the range of organisation in the group is comparatively slight. ‡

Returning once more to the vermean axis, we must next examine the upper third, the region above the origin of the Arthropoda. Near this point, and distinctly below the Annelides, is placed, on a side branch, the group Discophora or Hirudinea. It is possible that this may not be the true

* *Ann. and Mag. Nat. Hist.*, v. xii, p. 146 (1868).

† See Packard, *Guide to Study of Insects*, p. 105 (New York, 1876).

‡ In regard to the modifications of the larval condition, and the meaning of the metamorphosis of insects, see Lubbock's *Origin and Metamorphosis of Insects*, Nature Series (1874).

position of this somewhat obscure group, and when fuller knowledge as to its affinities has been acquired, it may turn out that the Discophora are really allied, not to the higher worms, but to the Platyelmia.*

From the ancestral Chætopoda, which compose this upper part of the vermean axis, the Oligochæta probably diverged in one direction, and the small group Achæta (*Polygordius*) in another. The various larval stages in the development of *Polygordius* show how the metameric segmentation, which is found in all the Chætopoda, was acquired in their ancestral history. Beginning with the Trochosphere stage (fig. 18), successive segments are formed at the post-

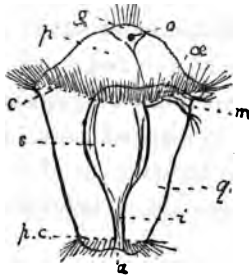


Fig. 18. Trochosphere. *p*, præ-oral lobe; *g*, post-oral or abdominal part of body; *e*, præ-oral circle of large cilia; *p c*, perianal circle of cilia; *m*, mouth; *œ*, oesophagus (stomodæum); *s*, stomach; *i*, intestine; *a*, anus; *g*, supra-oesophageal ganglion; *o*, eye-spot.

erior end of the body, gradually converting it into an elongated worm-like form, while the greater part of the original Trochosphere remains as the head region of the adult worm. In the Oligochæta and the Achæta no appendages are present, although in the former there are chitinous bristles (*setæ*) which project from the body wall. The primitive Oligochæta have diverged into several small groups, all of which are hermaphrodite, and possess highly specialised reproductive organs, more or less resembling those of *Lumbricus*.

* See Bourne, *Quart. Journ. Mic. Sc.*, vol. xxiv, No. xcv, p. 493 (1884).

Above this point the ancestral Polychæta must have acquired parapodia, the characteristic lateral appendages of the Annelides, upon which the bundles of setæ are borne. Various processes more or less of a sensory nature were also developed from the anterior end of the body (the præ-oral lobe), making it more of a specialised head. From this ancestor or some very similar form must be derived the curious little group of Myzostomida* which are found as ecto-parasites on the Crinoidea. They are certainly degenerate, and have been much modified since they left the main stem.

The series of ancestral Vermes finally terminates by breaking up into the progenitors of the numerous closely-allied groups of Polychæta now existing. These are therefore the highest members of the large and very heterogeneous phylum Vermes. Unlike the Oligochæta they are nearly all dioecious and marine forms, and have no highly specialised reproductive organs. In some of the groups (Tubicolous forms) a considerable amount of heteronomy is exhibited.

There remains now only the great and important phylum Chordata, which contains the whole series of vertebrate animals. The ancestral Chordata as we have already seen arose from the main axis of the Vermes rather low down. Hubrecht† maintains that there is a closer relationship between the Chordata and the Nemertida than my table shows; he regards the sheath of the protractile proboscis of the Nemertean as being the origin of the notochord, and considers that the Proto-Chordata arose from the Nemertida. Semper‡

* Beard, *Mitthl. Zool. Stat. Neapel.*, Bd. v., p. 544 (1884); and also L. von Graff, *Challenger Zoological Reports*; "The Myzostomida," vol. x, part xxvii (1884). From the adult anatomy Graff considers the Myzostomida as being allied to the Tardigrada.

† *Quart. Journ. Micros. Sc.*, vol. xxiii, no. xci, p. 349, July, 1883.

‡ *Arbeit. a.d., Zool.-Zoot. Instit.*, Würzburg, vols. ii and iii (1875-77).

and others on the contrary regard the Chordata as being derived from some group of the Annelida, chiefly on account of the similarity in their nephridia. I prefer to look upon the Proto-Chordata as having arisen from a more generalised form than either the Nemerteans or the Annelides. Their point of origin was certainly very far back, and may have been even lower down on the vermean axis than its position in the table. From the striking resemblance between the respiratory organs of *Balanoglossus* and those of some of the lower Chordata it is extremely probable that the Proto-Chordata started from ancestral Enteropneusta, and it has been already seen (page 40) that the Enteropneusta and the Echinodermata probably possessed a common ancestor outside the vermean series, consequently the Proto-Chordata, the Enteropneusta, and the Echinodermata most probably diverged from the main axis together as a branch which very soon gave off the first ancestors of the Chordata in one direction and the primitive Echinoderms in another.

The early Proto-Chordata had probably a worm-like segmented body (fig. 19), with a ventrally placed mouth in front

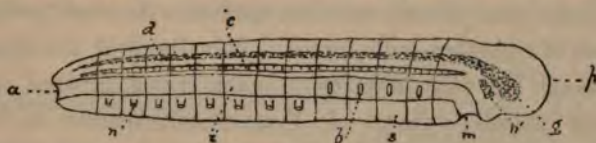


Fig. 19. Hypothetical ancestor of the Proto-Chordata. *a*, anus; *b*, anterior respiratory part of the alimentary canal; *c*, notochord; *d*, dorsally placed nervous system; *g*, supra-oesophageal ganglion forming part of brain; *i*, intestine; *m*, mouth; *n*, nephridium; *n'*, modified anterior nephridia (hypophysis cerebri?); *p*, front end of body formed of præ-oral lobe; *s*, one of the segments or metameres.

of which projected a large præ-oral lobe. The anterior portion of the alimentary canal had become respiratory in function by giving off a series of lateral diverticula which were placed in communication with the exterior by a series of vertical slits on the side of the body. Renal organs were present in the form of paired nephridia, placing the coelom in

communication with the exterior. Possibly, as Sedgwick* has suggested, the gill slits may, like the nephridia, be merely specialised parts of the original coelom, which was probably formed as a series of diverticula from the archenteron. The nervous system in place of being concentrated in a pair of cords, running more or less ventrally, as in all the higher Vermes and most of the groups derived from them, appears in the primitive Chordata to have moved dorsally (probably in consequence of some peculiarity in the habits or mode of life of the animal), so that eventually the two bands came to occupy a position above the alimentary canal and in the median dorsal line (compare fig. 13, E, and fig. 19). The anterior portion of the primitive nervous system (as seen in the vermean ancestor) which occupied the præ-oral lobe remained as the foremost part of the Chordate nervous system, which no longer crossed the alimentary canal (as it does in the higher Vermes and Arthropoda) but lay entirely upon its dorsal side. The chief modification in the structure of the Proto-Chordata was the formation of a stiff axis, the notochord, running longitudinally between the alimentary canal and the dorsal nervous system. It was probably formed of endoderm cells from the dorsal wall of the alimentary canal, but what its primary function was, or what organ in any existing group of Vermes corresponds to it is unknown.†

The lowest forms of the Chordata which we know are the Urochorda or Tunicata, but they are certainly a degenerate group which diverged from an ancestral Proto-Chordate more or less resembling *Appendicularia*, or better still, the tailed larval Ascidian. In these forms the notochord

* *Quart. Journ. Micros. Sc.*, vol. xxiv, No. xciii, p. 43.

† Hubrecht (*Quart. Journ. Micros. Sc.*, vol. xxiii, July, 1893,) has suggested that it was derived from the sheath of the proboscis of the Nemerteans.

is limited to the posterior part of the body, and does not extend forwards into the region occupied by the chief parts of the nervous system and alimentary canal. Whether this is the result of degeneration or indicates the primitive condition of the notochord in the Proto-Chordata is uncertain. Probably it is to some extent at least the result of degeneration or adaptation of the primitive Tunicata to surrounding conditions.

It may readily be imagined that these free-swimming surface organisms might find it advantageous that the alimentary canal, which performed both nutritive and respiratory functions, and the main part of the nervous system in connection with which sense organs were being developed, should be as much as possible concentrated in the anterior part of the body so as to leave the posterior part free to become modified into an efficient locomotory organ. Under such circumstances it would be natural that the notochord, the sole internal skeleton, should be restricted to the posterior part of the body where it would form an axis around which the muscles were placed.

From this ancestral Tunicate (fig. 20), represented at the

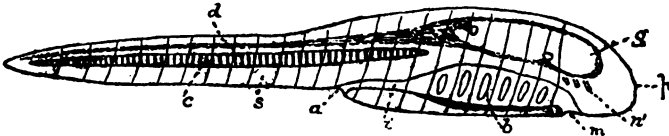


Fig. 20. Hypothetical ancestor of the Tunicata. *m*, mouth; *c*, notochord; *b*, anterior respiratory part of the alimentary canal; *d*, dorsally placed nervous system; *a*, anus; *s*, one of the segments or metameres; *i*, intestine; *g*, anterior ganglionic part of the nervous system; *p*, prae-oral lobe forming front of head; *n'*, anterior nephridia forming neural gland (hypophysis cerebri?).

present day by the Appendiculariidae two diverging lines seem to have started, both showing degeneration. In the first the organism remained free-swimming but acquired the power of passing currents of water through its respiratory system of cavities in such a way as to propel itself through

the water. This resulted in the great enlargement of these cavities and the development in the body-walls of transversely placed bands of muscle which served to drive out with force the contained water. The posterior region of the body, or tail, being now superseded as an organ of locomotion, became suppressed, and thus the Thaliacea (*Salpa*, &c.) were evolved.

In the second ancestral line the animal changed its habits, and became sessile; and, just as we find the tailed larval Ascidian at the present day, after a short free-swimming existence, becomes attached, loses its locomotory organ, and undergoes other changes, so the ancestral Tunicate, when it settled down on some object to lead a stationary existence, went through a similar but gradual process of degeneration. The tail, with its contained notochord, being no longer necessary, became rudimentary and disappeared. The well-developed sense organs, which were most important to a locomotory organism, had become almost useless through the change of life, and they also became suppressed, and, as a result, the nervous system, which was in most intimate connection with the sense organs, underwent considerable degeneration. On the other hand, the alimentary canal, and especially its respiratory portion, became greatly enlarged and somewhat complicated. This resulted in the formation of an ancestral form somewhat resembling the Simple Ascidi-ans, and probably more like a solitary *Clavelina* than any other existing form. It is probable that this creature then acquired the power of reproducing by gemmation, so as to form small colonies, like those of the "Social" Ascidi-ans (*Clavelinidæ*). From this point two lines started. In one series of ancestors the power of budding was retained, and the members of the resulting colonies became more closely united. This led up to the Compound Ascidi-ans, which have branched out into many smaller groups. The other set

of primitive Social Ascidians gradually lost the power of reproducing by gemmation, and so became the first solitary or Simple Ascidians.*

The long line extending from the point of separation of the most primitive Chordate from the Enteropneusta upwards to the place where the ancestral Tunicata diverged, indicates the considerable amount of evolution which must have taken place in the series of Proto-Chordata. It was during this period that the notochord and other characteristic structures of the Chordata, some of which are referred to above, were gradually acquired.

The Cephalochorda (*Amphioxus*) are, like the Tunicata, degenerate, and probably their ancestors diverged from the main stem nearly at the same point. As the notochord extends to the anterior end of the body in the Cephalochorda, it is highly probable that its restriction to the posterior part in the Tunicate larva and the Appendiculariidæ is, as suggested above, the result of adaptation. The anterior part of the nervous system is in a degenerate condition in *Amphioxus*, and sense organs are very feebly developed. The whole head is in a most rudimentary condition, probably as the result of degeneration.

Above the Proto-Chordata† from which the Cephalochorda arose, important changes took place resulting in the formation of a series of ancestral forms which Balfour has called the Proto-Vertebrata. In this group the notochord was no longer the only skeleton, neural arches extending upwards at the sides of the dorsal nervous system had made their appearance in the mesoderm. The anterior part of the nervous system became more highly developed so as to form

* For the phylogeny of the Simple Ascidians, see Herdman, *Challenger Zoological Reports*, vol. vi, part xvi, p. 286 (1882).

† In this region of the primitive Chordata and the lower Vertebrata the phylogeny given by Balfour has been followed (see *Comp. Embryol.*, vol. ii, p. 271).

a brain in connection with which sense organs were evolved. Probably as a result of this, the anterior end of the body became greatly modified and a well-marked head was formed by the differentiation and partial fusion of some of the anterior segments, including those, possibly reduced in number, in which the gill-slits were present.

From the Proto-Vertebrata the Cyclostomata were derived. They are probably degenerate forms, and possibly represent what was formerly a large group of primitive Vertebrata. From these the primitive Fishes arose by a series of changes resulting in the forms which Balfour has called the Proto-Gnathostomata. In this group the internal skeleton became considerably increased. Cartilaginous branchial bars were formed in the intervals between the gill-slits. True jaws appeared for the first time in the history of the Vertebrata. The vertebral column and the skull, formed in the mesoderm around the notochord and the dorsal nervous system, became much more completely developed than they were in the Proto-Vertebrata from which the Cyclostomata diverged. Finally, paired fins, or limbs, made their appearance. Probably, as suggested by Balfour and others, these were first formed as continuous lateral fins, one extending along each side of the body from close behind the gill-slits to near the termination of the alimentary canal. Afterwards concentration took place at two points on each side, resulting in the formation of the primitive pectoral and pelvic fins, while the part between became suppressed.

The Proto-Gnathostomata is represented by the existing Elasmobranchii, a group which have probably undergone comparatively little change and are, therefore, of great value as showing many of the typical vertebrate systems in a more or less primitive condition. The Holocephali are the modified descendants of an offshoot from the primitive Elasmobranchs.

The main line then passed upwards towards the higher Fishes. This ancestral series above the common origin of the Elasmobranchii and Holocephali, is the Proto-Ganoidei of Balfour, * called *Pneumatocela* by Bridge † because the air-bladder probably first appeared as a distinct organ in this group. From it the primitive Ganoids and Teleosteans diverged together.

The Teleostei are the most highly differentiated group of Fishes, and have been derived from the ancestral Ganoidei. The endo skeleton which was cartilaginous in the Elasmobranchii and Proto-Ganoidei, becomes more or less completely ossified in the higher Fishes, and especially in the Teleostei. In many respects the Ganoidei more closely resemble the common ancestry. They have separated into two groups, of which one retains in a less modified condition the primitive characteristics, while the other resembles the Teleosteans in the differentiations which have been effected. The Teleostei have been evolved into a number of distinct groups, some of which have diverged considerably from the common ancestor.

The Dipnoi must be regarded as representing an offshoot from the Proto-Ganoidei at the point where the common ancestors of the Ganoids and Teleosteans diverged from the line leading upwards to the higher Vertebrata. In some respects the Dipnoi exhibit features seen in the less modified Ganoidei and the Elasmobranchii, and in virtue of such characters they are persistent Proto-Ganoids; but on the other hand, the Dipnoi show in some points that they have undergone evolution in the direction of the line leading towards the primitive Amphibians. The most important character in which they exhibit an advance upon other groups of Fishes is the development of the air-bladder, which

* *Comp. Embryol.*, v. ii, p. 272.

† *Phil. Trans.*, 1878, Part ii.

in Ganoids and Teleosteans is mainly hydrostatic in function, into an accessory organ of respiration, which corresponds to the lungs of higher Vertebrata.

One of the most important changes which took place in the series of ancestral forms leading upwards from the top of the Proto-Ganoidei was the conversion of the ichthyopterygium, or fin-like limb, found in Fishes, into the cheiropterygium, or true limb, characteristic of higher Vertebrates. This change was probably effected by the elongation of the basal cartilage (metapterygium) of the fin to form the primitive humerus or femur, which became directed outwards from the body instead of lying more or less parallel with it. The other skeletal elements of the cheiropterygium are probably derived from modified fin rays.* The group in which this higher form of limb was first developed is Balfour's Proto-Pentadactyloidei. This must have split up into two lines of descent; the one forming the common ancestors of the Amphibia and the Labyrinthodontia, and the other leading upwards to higher forms—the Proto-Amniota.

The Urodelous Amphibia probably represent with comparatively little modification the first of these two ancestral lines. Lungs had now become completely developed, and their establishment as the chief respiratory organs had caused changes in the course of the circulation and in the structure of the heart. The Anura are a somewhat more modified group which have sprung from the Urodela, while the Gymnophiona are clearly degenerate forms, which probably diverged from the ancestral Urodela. The extinct Labyrinthodontia may be regarded as a lateral offshoot from the primitive Amphibians.

The Proto-Amniota divided into two great series of ancestral forms, the primitive Sauropsida leading upwards to Reptiles and Birds, and the early Mammalia. Just below

* *Comp. Embryol.*, v. ii, p. 510.

this point of divergence may be placed the extinct Ichthyosauria and Plesiosauria as independent branches from the Proto-Amniota, between the ancestral Amphibia and Reptilia. Their position is however a little doubtful. They may possibly have arisen further back than they are placed in the table, and may really be offshoots from the Proto-Pentadactyloidei, close to, but independent of the ancestral Amphibia.

In the primitive Sauropsida, the epidermis must have come to take a prominent part in the formation of the exoskeleton. The internal skeleton also, and especially the skull, became more completely formed and more thoroughly ossified. This group then probably split into two ancestral series, of which the one eventually produced the Crocodilia, the Ornithoscelida, and the Aves; and the other the Dicynodontia, the Chelonia, the Pterosauria, the Lacertilia, and the Ophidia.

The latter branch must be regarded as the more direct continuation of the primitive Sauropsida, and is probably most nearly represented by the Lacertilia of the present day. They form the central group in the Reptiles just as the Urodela do amongst Amphibians. The Ophidia are a degenerate group of Reptiles allied to the Lizards; they may be regarded as having diverged from the ancestral Lacertilia. The extinct Pterosauria branched off from the Lacertilian stem further back, and became considerably modified; while the Chelonia and the extinct Dicynodontia diverged still earlier, and probably not far above the point where the primitive Sauropsida branched. The Chelonia and the Dicynodontia probably left the ancestral Lizards at much the same point, or they may possibly have had a short common ancestry. The Chelonia have become greatly modified, chiefly in respect to their exoskeleton and body-form.

The second main branch of the Sauropsida leads upwards to the extinct Ornithoscelida (Deinosauria), the Crocodilia being given off as a side branch in the direction of the other Reptilia, and rising to a rather higher level of organisation.

The Aves are derived from the Ornithoscelida, and are mainly distinguished from other Sauropsida by the modification of the epidermal exoskeleton into feathers. The extinct groups belonging to this region shew a most interesting series of transition forms between Reptiles and Birds, and most of the Ornithoscelida lead gradually up through various extinct forms known as fossils to the Birds of the present day.

The Saururæ (*Archæopteryx*) were more primitive than any existing forms, and possessed a long tail, to which however feathers were attached. From this group the remaining Aves, in which the tail is short and formed of coalesced vertebræ, have descended in two series: the Ratitæ, in which the sternum is retained in its primitive flat condition, and the Carinatae, in which it is provided with a more or less well developed keel. The Aves have become differentiated into a large number of groups which, however, show very little structural modification. They attain a higher level of organisation than any of the other Sauropsida.

The first ancestral Mammalia probably arose from the Proto-Amniota, at the base of the Sauropsida. Caldwell's* recent investigations show that the most primitive Mammals now existing differ from the Amphibia, and agree with Reptiles and Aves in having a large amount of food-yolk in the ovum. Very possibly, this character was acquired by the Proto-Amniota, and inherited by the two lines of descent (Sauropsida and Mammalia) into which that group divided.

* See *Nature*, vol. xxx, p. 577. 1884.

It was afterwards lost far back in the Mammalian series. It is, I think, more probable that the first Mammalia and first Sauropsida diverged from a common ancestral stock in which the ovum had much food-yolk, than that the Mammals were derived from some group of the Sauropsida. The arrangement shewn in the table, besides taking account of the condition of the ovum in the Monotremata, also explains the very decided Amphibian characteristics of the Mammalia pointed out by Huxley,* such as the condition of the pelvis, the skull, and some other parts of the skeleton, if these Amphibian characters can be regarded, as I think they may, as being found in the Proto-Pentadactyloidei, from which both Amphibia and Proto-Amniota are derived. If this view is correct, then the features in which Mammalia resemble Amphibia are really ancestral Proto-Pentadactyloidean characteristics, and any in which they agree with Sauropsida only were acquired later by the Proto-Amniota.

The ancestral Mammals,—which must have developed mammary glands for the nourishment of the young, while the epidermic exoskeleton assumed the form of hair, and the left fourth aortic arch became the chief artery leaving the heart,—are most nearly represented at the present day by the Monotremata, a group in which the brain and some parts of the skeleton exhibit a lower stage of organisation than is found in other Mammalia. The oviducts also remain in the primitive condition of two tubes opening independently into a cloacal cavity, and the mammary glands are not well developed. The few existing forms belonging to the Monotremata are probably the representatives of a group which diverged from the earliest Mammals, and to which Huxley† has given the name Prototheria. The present Monotremata are doubtless somewhat modified, but retain the characters of the

* *Proceedings Roy. Soc.*, v. xxviii, p. 395 (1879).

† *Proceedings Zool. Soc.*, for 1880, p. 649.

Prototheria sufficiently to show that they are distinctly below any other groups of the Mammalia.

The Marsupialia may also be regarded as the existing representatives of an ancient group which diverged from the ancestral stem far back, but above the origin of the Prototheria. This group is Huxley's Metatheria; while all the remaining Mammalia, the descendants of the ancestral series, after the separation of the Prototheria and Metatheria, are the Eutheria.

The existing Marsupials show in their anatomical characters a condition intermediate between that of the Prototheria and that found in the Eutheria. The mammary glands in particular are much more highly developed than they are in the Monotremata; but in the structure of the brain and some parts of the skeleton they are still distinctly below the other groups of the Mammalia. The Marsupialia, although retaining the essential characters of the Metatheria, have probably undergone considerable evolution, which has affected the less important points of structure, and given rise to several distinct groups presenting differences mainly in external features, and evidently related to their very diverse habits.

In the evolution of the early Eutheria, the third group of ancestral Mammalia,* one of the most important changes was the acquisition of the allantoic placenta for the nourishment of the embryo. The placenta is present in all of the Eutheria, which are therefore called "Placental Mammals," and is variously modified in the different groups.†

The Edentata were probably the first important divergent series from the ancestral Eutheria. The existing members

* For an account of the Mammalia see Flower's article "Mammalia," in *Encycl. Brit.*, 9th edition, v. xv, p. 347.

† For a comparative history of the Placenta, see Balfour, *Comp. Embryol.*, v. ii, p. 198.

of this group have become greatly specialised in accordance with their habits of life. Many extinct forms are known from their fossil remains, and it is probable that the Edentata were once a much larger group than they are now. They probably divided at an early period into several distinct branches, the representatives of some of which (*e.g.*, *Manis* and *Orycteropus*) are very different from the other members of the group. The existing Edentata ought probably to be considered as having degenerated somewhat.

The Sirenia are probably the remains of a degenerate offshoot from the older Eutheria above the point of origin of the Edentata. They are not closely related to any of the higher groups of Mammals, and, therefore, probably diverged before the Eutherian stem began to split up. In the Sirenia the hind limbs are wanting, hair is almost entirely absent from the skin, and the body is modified to suit the aquatic habits of the animals.

The remaining groups of the Eutheria are all more or less closely allied to one another, but it is very difficult to determine the lines of their evolution. As they can be nearly all traced back to a generalised form, with characters which may have been common to the ancestral Ungulata, Carnivora, and Prosimiæ, the probability is that the main stem split up soon after the separation of the primitive Sirenia, into various branches leading to the main groups of higher Mammals. These may be arranged in two series, the one consisting of the ancestral Ungulata, from which probably the Cetacea, Hyracoidea, Proboscidea and Rodentia arose at different points in the series; and the other comprising the common ancestors of the Carnivora, Insectivora and Cheiroptera, and of the Prosimiæ and Primates.

The former of these two series is shown in the table as diverging to the left and leading upwards through a long series of ancestral Ungulata. The Cetacea probably arose

from near the base of this branch, but have diverged greatly. Like the Sirenia (with which they have no direct or close relationship) they are modified to suit an aquatic existence, and in some respects—especially in the condition of the limbs and the almost total absence of hair—they exhibit considerable degeneration.

The primitive Ungulata were continued upwards into the ancestors of the Artiodactyla and Perissodactyla, the two groups into which the existing Ungulata fall, and of numerous extinct groups which unite the Artiodactyla and Perissodactyla, or diverge from them to varying extents. The ancestral Rodentia, Hyracoidea and Proboscidea, and many extinct groups known by their fossil remains, arose from the series of primitive Ungulates.*

The Rodentia are the most important of these divergent branches. They have undergone very considerable evolution since their origin, and are now a well-defined group of large size, and containing a number of distinct families. But a passage can be traced through the extinct forms *Mesotherium* and *Toxodon* from undoubted Rodents to typical Ungulates. Similarly the Proboscidea, although now a very isolated group, may be joined to the Ungulata by the extinct Proboscidea, the Dinotheria, and the Dinocerata. The primitive Hyracoidea probably arose from the Ungulate stem, close to the point of origin of the Proboscidea, but diverged in a different direction, and the group as it is now known (*Hyrax*) occupies a very isolated position. Thus from the primitive Ungulates, which arose from the generalised Eutherian, ancestral lines of descent diverged towards such very different groups as the Cetacea, the Hyracoidea, the various series of living and fossil Ungulata, the Proboscidea and the Rodentia; but the relations of these different

* See Flower, article "Mammalia" in *Encycl. Brit.*, 9th edition, v. xv, p. 372.

branches to one another, and their probable lengths and directions, are still very obscure.

The second main branch of the higher Mammalia probably split far back into the ancestral forms of two great groups—the first of which became evolved into the Cheiroptera, the Insectivora, and the Carnivora; while the second was the stock from which the Prosimiæ and the Primates have descended.

In the first of these series, the extinct Creodontia probably represent the early ancestral Carnivora, from which the Insectivora diverged. The Cheiroptera agree with the Insectivora, and with the primitive Carnivora in many respects. Possibly they may have arisen as a side branch from the Insectivora, and not from the early common ancestors of Carnivora and Insectivora, as shown in the table. The Cheiroptera have undergone great modification since they diverged, the anterior extremities having become converted into organs of flight. The Bats now existing fall naturally into two main groups, which however have probably had a long common ancestry.

The Insectivora retain many of the characters of the primitive Carnivora, from which they are descended. They have undergone less modification than either the Cheiroptera or the Carnivora, and some of them probably represent better than any other existing forms the primitive higher Mammal from which all the groups above the Sirenia have been derived. The aberrant genus, *Galeopithecus*, is best placed as a side branch from the Insectivora.

The primitive Carnivora must have divided into two ancestral series, the one leading to the Carnivora proper (Fissipedia), while the other diverged to the Seals and their allies (Pinnipedia). The Fissipedia are probably the most direct descendants known of the ancestral Carnivora. They have undergone a considerable amount of evolution, and have

split up into three groups, the *Æluroides* (Cats, etc.), the *Cynoidea* (Dogs, etc.), and the *Arctoidea* (Bears, etc.). Some of the extinct *Carnivora* shew transition forms between these now distinct sections. The *Pinnipedia* have been greatly modified in accordance with their aquatic habits. They are most nearly allied to the *Arctoid* section of the *Fissipedia*, and, notwithstanding the great modification, a passage may be traced from the typical Seals (*Phocidæ*) through *Trichechus* (Walrus) and *Otaria* (Sea-Bear) to the true *Carnivora*.

Turning now to the important line leading upwards to the *Primates*, the highest Mammals, we find that soon after diverging from the primitive *Carnivora* a side branch is given off which leads outwards to the *Prosimiæ* (Lemurs). This group has not undergone much evolution, and as it probably arose very far back, the existing members may be taken as representing the early ancestral forms of the *Primates*. A considerable gap exists, however, between the Lemurs and the *Primates* as now known. Some fossil *Prosimiæ* show resemblances to the primitive *Ungulates*, but such features may be merely characteristics inherited by both groups from the generalised higher Mammal which was their common ancestor. Certain North American fossil forms are in some respects transitional from the *Prosimiæ* to the *Primates*. Probably they represent the earlier and less specialised Lemurs, or possibly the ancestral *Primates* from which the Lemurs arose. *Tarsius* and *Chiromys* must be regarded as forming divergent branches, while the rest of the existing *Prosimiæ* do not exhibit much modification.

The *Primates* are shown in the table as forming five more or less divergent branches from a main stem, viz., the *Arctopithecii* (*Hapalidæ* or *Marmosets*), the *Platyrrhini* (*Cebidæ* or *American Monkeys*), the *Cynomorpha* (*Cercopithecidæ* or *Old-World Monkeys*), the *Anthropomorpha* (*Simi-*

idæ or Man-like Monkeys), and the Anthropida (Hominidæ or Men). The Cynomorpha and the Anthropomorpha together constitute the group Catarrhini.

Of these the Arctopithecæ probably diverged first from the ancestral Primates. They form a small group which has not undergone any great modification. The Platyrrhini and the Catarrhini shew very marked differences, and consequently must have diverged greatly from the common ancestral series. Probably the Platyrrhine branch was given off first, and it has not risen to so high a level of organisation as the remaining Primates have.

The common ancestors of the Catarrhini and the Anthropida, after the separation of the primitive Platyrrhini, must have acquired the narrow partition between the nostrils and the arrangement of teeth characteristic of man and some of the higher monkeys. This ancestral series then gave rise to two divergent lines of descent, the one leading to the Catarrhini, and the other to the first men.

The Catarrhine branch probably split at an early period into two parts—a lower, which has resulted in the Cynomorpha, a group containing all the ordinary Old-World Apes, quadrupedal forms with ischial tuberosities and usually a long tail; and a higher, represented by the Anthropomorpha or Anthropoid Apes, which assume a semi-erect position and have no tail. This last group includes four genera which are decidedly the highest of Apes, and those which approach most nearly to the Anthropida, although, as may be seen from the table, they are not in any sense ancestral forms. They are: *Troglodytes* (the Chimpanzee), *Gorilla*, *Simia* (the Orang), and *Hylobates* (the Gibbons).

The Anthropida, the highest product of evolution, probably arose from the ancestral Catarrhini. It is possible, however, that the point of origin was on the Catarrhine branch, near the place where the Cynomorpha and Anthro-

morpha diverged. In the table, the more primitive and less specialised ancestor has been adopted as the starting point. From this early Anthropoid, or generalised Catarrhine Ape, a series of forms arose, in which the erect position, accompanied by slight adaptations of the vertebral column, was more and more perfectly assumed, while, at the same time, the proportion of the upper to the lower limb, and of the facial to the cranial region of the skull, was reduced, the hallux or great toe became relatively longer, and the power of bringing it into opposition with the other toes was gradually lost. Finally, by the reduction in size of the male canine teeth, and the modification of the hairy covering of the body, these ancestral forms were converted by slight changes into the primitive man.*

This remote progenitor, who lived at least as far back as Pliocene times, was like all other organisms subject to the laws of variation and heredity, and, under the influence of Natural Selection became gradually evolved into the ancestors of the various races or varieties of the genus *Homo*. There is no reason to regard these races as constituting more than one species.

* For an account of the Anthropoid Apes, and their relations to the Anthropida, the student should consult Huxley's *Anatomy of Vertebrated Animals*, p. 474, and Darwin's *Descent of Man*, chapters ii and xxi.

EXPLANATORY.

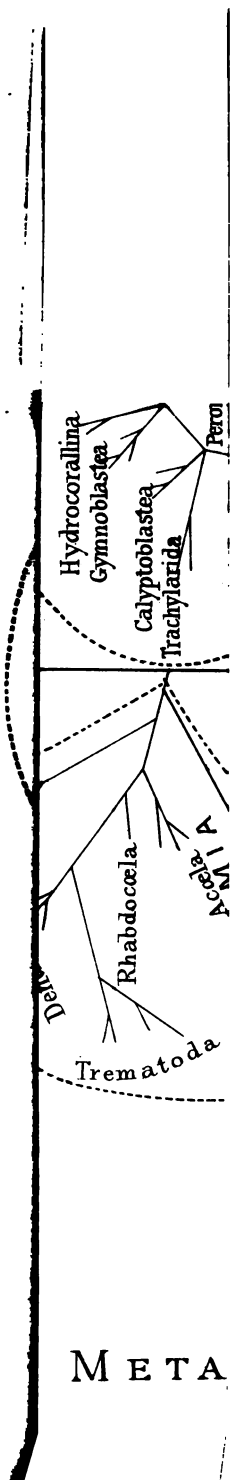
THE lowest organisms are placed at the foot of the Table, the highest at the top. The line, straight or zig-zag, traced from the very base upwards to any name indicates the probable course of the evolution of the group of animals to which the name belongs. If a line stretches upwards it shows an advance in structure; if it is nearly horizontal it means that little or no upward evolution has taken place; if it slopes downwards, that indicates degeneration or degradation. The proportional lengths and angles of the various lines are meant to represent roughly the amount and the nature of the evolution which has taken place.

In no case has the line representing the evolution of one group been allowed to pass through another group. All existing animals are represented as being at the *ends* of lines or branches.

Most of the larger groups or phyla have been enclosed in dotted red lines in order that their limits might be easily seen at a glance.

It is scarcely necessary to point out that horizontal lines could not be drawn across this table in such a way as to divide it into sections representing the Fauna of the various geological periods. In order to show that, a very different table would require to be constructed in which distance along a line stretching upwards from the base* would indicate merely the age of the group and not evolution or advance in organisation as in the present table. Degeneration could not be represented, and it would be impossible to distinguish except, perhaps, by colour, between groups which had undergone rapid evolution and those which had remained comparatively stationary.

* In such a table the Foraminifera and other groups of Protozoa would extend from the base to the top of the table, although they have undergone comparatively little evolution. Some of Haeckel's phylogenetic schemes (see *Generelle Morphologie der Organismen*, Berlin, 1866) are of this palaeontological nature and show the probable distribution in time of the various groups of animals and plants.



M E T A



